



The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea

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Abstract. New fossils of helodermatid squamates from the early Miocene of Nebraska prompted us to examine all known material actually or potentially referable to Helodermatidae. Although represented today only by two species ranging from southwestern United States south to Guatemala, the fossil record of Helodermatidae encompasses the Late Eocene of France, and the latest Paleocene to Recent of North America. If *Paraderma bogerti* Estes is a helodermatid, as we contend, Helodermatidae extends to the late Cretaceous in North America. Extinct lanthanotines and varanines from the late Cretaceous of Mongolia, together forming the sister taxon (Varanidae) of Helodermatidae, confirm the antiquity of these groups.

From early in their history the principal morphological specialization of helodermatids has been their powerful, stoutly constructed jaws capable of crushing large prey; living *Heloderma* may consume proportionally larger prey than any other squamate aside from certain snakes. Teeth grooved for venom delivery appear in all Cenozoic helodermatids, but that attribute is fully elaborated only in the two extant species, *Heloderma horridum* and *H. suspectum*.

Within Helodermatidae, *Eurheloderma gallicum* Hoffstetter is distinguished by a markedly constricted parietal, an attribute that may be ancestral for Varanoidea. A similarly constricted helodermatid parietal is herein reported from the latest Paleocene of Wyoming. Because of the diagnostic triangular frontal bones, we reassign the late Oligocene–early Miocene species *Heloderma matthewi* Gilmore to a new taxon, *Lowsaurus*. We reexamine its contemporary, *Heloderma texanum* Stevens, from the early Miocene of Texas, and infer its relationship with living *Heloderma* according to osteoderm morphology and a wide basal opening of the venom groove.

By necessity, our evaluation of helodermatid phylogeny requires a review of character states found in their sister taxon, Varanidae (Lanthanotinae + Varaninae). We clarify a number of morphological features such as the structure of the intramandibular joint and retraction of the bony nares. Monophyly of the group Helodermatidae + Varanidae is easily documented, and we restrict the name Varanoidea to that taxon. However, the phylogeny of a more encompassing taxon, Platynota, is ambiguous and we recommend that designation only as a term of convenience, to include varanoids and those other taxa with which they have been traditionally associated ("Necrosauridae," Mosasauridae, Aigialosauridae, and Dolichosauridae).

Our interpretations of helodermatid phylogeny are consistent with morphological evidence, and with behavioral and ecological aspects of their feeding biology.

INTRODUCTION

Prior to Gilmore's (1928) review of the fossil lizards of North America, nearly all lizard remains with hexagonal cephalic osteoderms had been assigned to Helodermatidae. Gilmore (1928) restricted the taxon to the two living species, *Heloderma suspectum* Cope (Gila monster) and *H. horridum* Wiegmann (Beaded lizard), and a new species, *H. matthewi* Gilmore, based on a partial maxilla from the Middle Oligocene

(Orellan) of Colorado that exhibited the group's unique dentition: grooved teeth used for venom delivery. Fossils previously assigned to helodermatids (e.g., by Nopsca 1908) were referred to Anguidae (viz., Glyptosaurinae; see Sullivan 1979). After Gilmore's (1928) revision, no additional fossils of helodermatids were described until 1957 when *Eurheloderma gallicum* Hoffstetter was reported from the late Eocene/early Oligocene Phosphorites du Quercy of France (Hoffstetter 1957). Subsequently, more material of *E. gallicum* was reported from the phosphorite locality at Escamps (DeBonis et al. 1973). Currently, the species is represented by maxillae, a dentary, pterygoids, parietals and vertebrae.

In the last decade, additional fossils of North American helodermatids were found in deposits of the White River Formation of Colorado (late Oligocene–Whitneyan). This material consists of dentaries, maxillae, frontals, parietals and other cranial fragments, all of which Yatkola (1976) referred to *Heloderma matthewi*. In his discussion of the helodermatid fossil record, Yatkola concluded that all lizards possessing teeth grooved for venom conduction were sufficiently similar to be included in a single genus, *Heloderma*. He thus relegated *Eurheloderma* Hoffstetter to synonymy.

Shortly after Yatkola's (1976) paper was published, Larry Martin (University of Kansas) provided us with a frontal bone and two vertebrae collected from early Miocene deposits of Nebraska. These fossils are helodermatid, as described below, and are comparable to other middle Tertiary specimens that have been assigned to *Heloderma matthewi*, but we believe that they comprise a taxon diagnoseable from *Heloderma* proper. In the early Miocene, *Heloderma* was represented by *H. texanum* Stevens, a species described from a remarkably complete skull found in the Castolon Local Fauna of Big Bend, Texas (Stevens 1977); however, its relationship with other helodermatids was not considered at the time of its description (Stevens 1977).

Finally, Bartels (1983) has described a varanoid parietal collected from the latest Paleocene of the Bighorn Basin, Wyoming. That fossil, too, is from a helodermatid, as discussed below.

McDowell and Bogert (1954) were the first to place helodermatids in a systematic framework that combined them with *Varanus* and *Lanthanotus* as a group distinct from other extant anguimorph squamates. McDowell and Bogert (1954) altered Romer's (1956) classification by removing *Lanthanotus* from Helodermatidae and placing it closer to Varanidae. They assigned Helodermatidae to Varanoidea instead of Anguioidea (Diploglossa), and recommended the designation "Varanoidea" over "Platynota." Hence, Varanoidea included Varanidae, Lanthanotidae, Helodermatidae, and the extinct families Dolichosauridae, "Aigialosauridae" and Mosasauridae. With some modifications, Rieppel (1980a) corroborated their conclusions, but used the name Platynota for this taxon. In that paper and in a companion study on the postcranial osteology of *Lanthanotus* (Rieppel 1980b), he regarded the three extant families as a monophyletic assemblage within the more inclusive Platynota. Elsewhere, Gauthier (1982) discussed Varanoidea with reference to the articulation between the dentary and post-dentary bones, a character complex providing insight into anguimorph phylogeny.

The evolutionary history becomes cluttered, however, in consideration of several fossils from the late Cretaceous of North America and Asia, and the Paleogene of Europe that can be interpreted as at or near the base of helodermatid and varanoid phylogeny. For example, Estes (1964) proposed Parasaniwidae to accommodate two taxa from the late Cretaceous Lance Formation of Wyoming: *Parasaniwa wyomingensis* Gilmore and *Paraderma bogerti* Estes. More recently Estes (1983a) synonymized Parasaniwidae with the more inclusive designation Necrosauridae Hoffstetter, a family constituted by Estes to include *Necrosaurus*, *Parasaniwa*, *Eosaniwa*, *Provaranasaurus*, and *Colpodontosaurus*.

Paraderma bogerti is in ways similar to necrosaurids but remains even more problematical, primarily because it is so poorly represented by fossils. We regard it as the earliest known member of Helodermatidae.

Borsuk-Bialynicka (1984) described several new anguimorphs collected from Upper Cretaceous deposits of Mongolia. Two of these, *Proplatynotia longirostrata* and

Gobiderma pulchrum, she referred to as “necrosaurian grade lizards,” primitive platynotans whose relationships among anguimorphs remain problematic. Furthermore, *Gobiderma* possesses a few features described as *Heloderma*-like. Besides these taxa, Borsuk-Bialynicka (1984) reported the first known remains of a fossil lanthanotine, *Cherminotus longifrons*, a new varanine, *Saniwides mongoliensis*, as well as additional material of the enigmatic varanid *Telmasaurus grangeri* Gilmore. These new varanoids, though difficult to place unambiguously, do suggest that the lineages represented by *Heloderma*, *Lanthanotus* and *Varanus* are of considerable antiquity. The incomplete nature of the Cretaceous fossils makes their early history difficult to resolve.

The discovery of these new helodermatid and varanid fossils, and our interpretation of novel characters, inspired this review of helodermatid phylogeny. The paper is organized into three parts. Part I reviews the diagnosis of Varanoidea in an attempt to clarify those characters that have been troublesome and ambiguous. We then (Part II) describe the new helodermatid fossils from the early Miocene of Nebraska, and discuss another from the latest Paleocene of Wyoming. In light of these we reinterpret *Heloderma texanum* and those fossils previously assigned to *H. matthewi* in a discussion of the diagnostic features of Helodermatidae. A phylogeny based on this evidence is presented. Having this background, together with information from Part III on their natural history, we propose that the principal specialization of helodermatid squamates is a distinctive feeding mode. This is readily observed in the stout jaws and sturdily constructed skull architecture designed for crushing large prey. Venom delivery occurs in the more derived species as a superimposed specialization. For these reasons we will argue for the inclusion of *Paraderma bogerti* in Helodermatidae. We conclude our presentation of helodermatid phylogeny based on morphology by demonstrating (Part III) some concomitant associations with the natural history, behavior, and feeding biology of captive and wild animals.

MATERIALS AND METHODS

Museum abbreviations of catalogued specimens:

- AMNH American Museum of Natural History, New York
- BHB Bayard H. Brattstrom, California State University, Fullerton
- KU University of Kansas Museum of Natural History, Lawrence
- KUVP University of Kansas, Vertebrate Paleontology, Lawrence
- MVZ Museum of Vertebrate Zoology, University of California, Berkeley
- PU Princeton University
- REE Richard Etheridge, San Diego State University
- SDSNH San Diego Natural History Museum
- TM Texas Memorial Museum, University of Texas, Austin
- UCMP University of California Museum of Paleontology, Berkeley
- UMMZ Museum of Zoology, University of Michigan, Ann Arbor
- UMMP Museum of Paleontology, University of Michigan, Ann Arbor
- UNSM University of Nebraska State Museum, Lincoln
- WP William Presch, California State University, Fullerton

Specimens Examined.

Skeletons of Recent Heloderma.—*H. horridum* AMNH 7216, 56439, 57768, 57863, 64128; MVZ 79417; SDSNH 8906, 55596, 59469; REE 802; UCMP 117512, 118927, 118928, 123071, 131263, 131264, 131265; UMMZ 149609, 181151, 181637; WP 648.

H. suspectum AMNH 56432, 66998, 71082, 71864, 72646, 72748, 72908, 72999, 73771, 74777, 74778, 109521; BHB 802, 3158; KU 129, 1173, 13998, 23002–23010, 78906; MVZ 6313, 29398, 64208, 95990, 128983; SDSNH 55287, 57084, 62991; REE 1030, 1026, 1029; UCMP 117511, 131261, 131262; UMMZ 128115, 130160, 149610, 149611, 173549, 173550, 178528, 178529, 180467, 181130, 181638, 181640, 181641; WP 120, 235, 649, 650, 651, 652, 687 (skull only).

Two frozen specimens of *H. suspectum* were available for dissection (SDSNH uncat.).

Skeletons of Recent varanids. — *Lanthanotus borneensis* REE 1445. *Varanus bengalensis* SDSNH 57081, 60436, 60437; UMMZ 128572, 130172. *V. exanthematicus* REE 1987; UMMZ 151113. *V. komodoensis* UMMZ 149612. *V. nebulosus* SDSNH 26058. *V. niloticus* SDSNH 55279, 63815; UMMZ 149613. *V. prasinus* SDSNH 57082, 59468, 60438, 60441. *V. salvator* SDSNH 57080; UMMZ 128112, 128113, 130167, 149614, 149615, 168411, 173096. *V. varius* AMNH 28698.

Fossils. — *Paraderma bogerti* UCMP 49939, 49895, 49940, 54199, 54213, 54261 (holotype); *Heloderma matthewi* AMNH 990A (holotype), KUV 7652, 49651, 49652, UNSM 50011; *H. texanum* TM 40635-119, -123 (holotype), 40635-137, -138, -140; *Eurheloderma gallicum* PU 12280; helodermatid parietal UMMP 74619.

Osteological terminology follows Estes (1983a), McDowell and Bogert (1954) and Meszoely (1970).

Our method of assessing character polarity follows the recommendations of Maddison et al. (1984). Monophyletic taxa successively removed from Helodermatidae were consulted as the need arose. Although not formally considered in this analysis, the Mongolian Cretaceous varanoids described by Borsuk-Bialynick (1984) also were evaluated to help resolve cases of character ambiguity. In several instances, so noted, multi-state characters were recoded in order to achieve consistency in coding all characters in standard binary fashion (0 = ancestral; 1 = derived; 9 = missing data). A character matrix was compiled and subjected to computer analysis using Swofford's (1984) PAUP program installed at the University of Michigan, and PHYSYS available through the California State University system (CSU CYBER). The results of these procedures were used mainly as a check of our own analyses.

I. VARANOIDEA

Because our polarity assessment of helodermatid characters relies on their distribution first among Varaninae and Lanthanotinae and second among other anguimorphs, it is necessary to review the attributes of Varanoidea that others have considered diagnostic. This review collates a scattered literature on the subject, but essentially the purpose is for assessing relationships within helodermatids in the context of character distribution within their sister taxa.

The following characters (and character complexes) have been considered diagnostic for Varanoidea, several of which require comment. Parenthetical numbers denote the corresponding character(s) in Tables 2 and 3.

McDowell and Bogert (1954) (also Romer 1956):

A. *Loss of caudal autotomy* (52).

B. *More deeply cleft fore-tongue (notched not less than 20% of length)* (71).

C. *Intramandibular kinesis* (37–45). — The progressive development of intramandibular kinesis figured prominently in McDowell and Bogert's characterization of Varanoidea, and also has been discussed by Rieppel (1980a) and Gauthier (1982). In these and other studies several characters affecting mandibular kinesis have been identified: a truncated margin of the posterolateral edge of the dentary; surangular foreshortened anteriorly; splenial reduced anteriorly and posteriorly; anterior extension of the lateral and medial arms of the coronoid present, but not broadly overlapping the dentary; a tiny, free posteroventral process on the intramandibular septum (IMS); and a fibrous connection between the dentary and postdentary bones. These modifications appear to form a developmentally and functionally related complex of characters that distinguish the mandible of varanoids from all other anguimorph squamates. That is, there is at least some mobility of the dentary with respect to the post-dentary bones.

McDowell and Bogert (1954:108) believed that the principal modification in the evolution of intramandibular kinesis was the formation of a vertically truncated posterior margin of the dentary, such that the dentary overlaps little or not at all with the

post-dentary bones. In helodermatids, they thought (incorrectly) that the intramandibular hinge was absent (*H. suspectum*) or rudimentary (*H. horridum*) because the posterolateral edge of the dentary is not truncated in these species, the structure being more like the primitive anguimorph condition in having an obvious surangular notch at the posterolateral edge (Gauthier 1982). However, manipulation of freshly excised mandibles of both species of *Heloderma* demonstrated to us that the dentary can move freely through an arc of approximately 10° with respect to the post-dentary bones; similarly, the dentary of *Varanus prasinus* can be moved through an arc of approximately 17° . The splenial passes posterior to this joint in *Heloderma*. However, the splenial is quite thin and it simply bends during kinesis. By contrast, in varanines, and presumably lanthanotines, the splenial moves as a unit with the dentary. A vertically truncated posterolateral margin of the dentary (and splenial) is, therefore, not required for kinesis, although it apparently enhances mobility.

Our dissections indicate that the internal structure of the mandible at the coronoid juncture probably plays the most important role in facilitating movement in the lower jaw. In anguids and xenosaurids the surangular is long, tapers anteriorly and terminates inside the dentary well forward of the last tooth, as in most squamates (Gauthier 1982). The surangular bone is recessed laterally to receive a prominent overlapping portion of the dentary. Thus, a broad mutual overlap between the dentary and postdentary bones prevents flexure at the coronoid juncture. In varanoids, however, the surangular is not tapered, and the anterior end is truncated so that it barely reaches the posterior end of the tooth row. Accordingly, overlap between the dentary and surangular is restricted; the bones are secured to one another by a thick band of connective tissue rather than by the firm osseous connection seen generally in anguids, xenosaurids, and other squamates (Gauthier 1982).

Another feature of the mandible of some varanoids is the presence of a small notch in the posteroventral margin of the intramandibular septum (IMS). The anteroventral end of the surangular fits into this notch, thus restricting torque about the intramandibular joint. In Varanidae and some *Heloderma suspectum* this character has reversed, the notch being absent.

Preliminary developmental studies suggest that there are few neomorphic structures in the mandible of varanoids that promote kinesis; rather the action is accomplished by an apparently paedomorphic reduction in the extent of contact among the bones comprising the dentary/post-dentary articulation, as well as an incorporation of fibrous connective tissue into this joint.

D. *Maxillary tooth row not extending posteriorly below orbit* (27); *ectopterygoid elongate and contacting palatine to exclude maxilla from suborbital fenestra* (36).

E. *Bases of teeth expanded and infolded (plicidentine)* (24); *teeth sharply pointed, trenchant, recurved and widely-spaced* (25); *teeth without replacement pits, i.e., teeth develop outside tooth bases* (26) (see also Rieppel 1978).

F. *Partial retraction of nares, i.e., nasals barely or not at all in contact with prefrontals* (2,3,4).—McDowell and Bogert (1954) characterized helodermatids and all other platynotans as having retracted nares. That is, the external nares are elongated posteriorly such that they separate the nasal from the prefrontal and maxilla. Apparently, they based their conclusion regarding *Heloderma* on a specimen of *H. horridum* (AMNH 57863) that was also illustrated in their monograph (p. 36). This same illustration and the character itself was used later by Bogert and Martin del Campo (1956: 18). Rieppel (1980a) also included this feature as a character of Varanoidea. On AMNH 57863 the osteoderms had been removed from the left side of the skull to reveal a narrow slit in the posterodorsal end of the bony nares between the nasal, maxilla, prefrontal and part of the frontal, giving the appearance of "retracted" nares. However, in *Heloderma* extensive connective tissue occurs in the nasal-maxilla-prefrontal region that usually shrinks when the skull is prepared as a dry specimen. Depending on the degree of desiccation, the nasal bone can show varying degrees of separation from the maxilla and prefrontal. This appears to be the case with AMNH 57863. These bones have smooth narial margins in varanids and form true retracted nares: there is no

contact between the nasal and maxilla, and very little (*Lanthanotus*) or none (all other varanids) between the nasal and prefrontal. Anguids and xenosaurids exhibit broad contact of the nasal with the maxilla, but very little occurs in *Heloderma*. *Heloderma* does possess a broad nasal-prefrontal contact, as seen generally in squamates. Thus, moderately retracted nares occur in *Heloderma* by an anterior narrowing of the nasals, although the bones are not as reduced in length as they appear in *Lanthanotus* and *Varanus*.

Miller (1966):

G. Cochlear duct robust and broad, limbus elongate and heavily constructed (75).

Lécure (1968a, b):

H. Mesosternum absent (60).

I. Anterior process of interclavicle reduced or absent (59).—An anterior process of the interclavicle is absent in some species of *Varanus* (e.g., *V. niloticus*) but a short process is present in others (e.g., *V. griseus*; also *Saniwa*—personal observation). Lécure (1968a) and Rieppel (1980b) present conflicting evidence for *Lanthanotus*. Lécure (1968a: fig. 15) illustrated the interclavicle having a pair of horn-like anterior processes, whereas Rieppel (1980b:103) figured the structure without any sort of anterior process, the crossbar or lateral processes being a rectangular plate at the anterior end of the bone. In this respect, our specimen of *Lanthantus* (REE 1445) agrees with that figured by Lécure.

J. Clavicles gracile (58).

K. Ulnar nerve passes deep in forearm ("varanid condition") (76) (see Renous-Lécure 1973).

Hoffstetter and Gasc (1969):

L. Vertebrae with precondylar constriction (not listed).—Precondylar constriction of the trunk vertebrae is marked in *Varanus*, and hardly noticeable in *Heloderma*. In fact, McDowell and Bogert (1954) claimed that in *Heloderma* the vertebrae were not constricted anterior to the condyles. Rieppel (1980b) reported that *Lanthanotus* exhibits a condition very similar to that of *Heloderma*, wherein the precondylar constriction is present, but faint. Actually, this character can only be evaluated subjectively and we prefer not to consider it diagnostic of Varanoidea; undoubtedly it is a synapomorphy of *Varanus*.

M. Peduncles on cervical and caudal vertebrae supporting hypapophyses and chevrons, respectively (53, 54).—In following Hoffstetter and Gasc (1969) and his own observations, Rieppel (1980b) recorded the presence of cervical and caudal peduncles as a synapomorphy of *Varanus* and *Lanthanotus*. On the other hand, McDowell and Bogert (1954:124) stated that "Even the most primitive platynotan [*Heloderma*] has distinct pedicles for the caudal chevrons, as far as known, all platynotans have the chevrons freely articulated to the caudal centra." We concur with McDowell and Bogert. Whereas caudal peduncles are certainly most prominent on *Varanus*, they are not unique. They are present, albeit feebly, on our comparative skeletons of *Heloderma*, and in fact can be observed in other anguimorphs, such as *Xenosaurus*. The hyper-developed cervical and caudal peduncles of varanids, and the fact that neither the chevrons nor the cervical intercentra contact the centrum condyle, will distinguish this taxon, but the presence of caudal peduncles themselves will not diagnose Varanoidea.

Saint Girons (1976):

N. Large, anatomically differentiated sero-mucous gland on lower jaw [Gland of Gabe (Kochva 1974)] (73).

O. Calyciform duodenal cells of muco-serous rather than mucous type (74).

Gabe and Saint Giron (1976):

P. *Double lacrimal canal* (80).

Rieppel (1980a, b):

Q. *Epicoracoid does not contact the suprascapula and mesoscapula to enclose a scapular fenestra* (55) (also Camp 1923).

R. *Narrow-based bodenaponeurosis attached to caudomesial edge of coronoid process (except Lanthanotus)* (69).

S. *Insertion of M. episterno-cleido-mastoideus reaches supratemporal process of parietal* (62).

T. *M. adductor mandibulae externus profundus (3b-layer) originates from supra-temporal only* (64).

U. *Origin of M. geniomyoideus is deep to M. genioglossus medialis* (65).—In *Lanthanotus* the origin of the *M. geniomyoideus* is superficial relative to the *M. genioglossus medialis*, as in all xenosaurids and anguoids; therefore the condition appears ancestral. In *Varanus*, however, the muscle has shifted its origin and is entirely deep to the *M. genioglossus medialis*. In *Heloderma* the origin is transitional in that some fibers still retain an attachment with the symphyseal tip of the dentary, whereas others are deep to the *M. genioglossus medialis* (Rieppel 1980a). We consider the condition in *Lanthanotus* secondary in this regard.

V. *Insertion of M. levator pterygoidii does not extend posteriorly beyond columellar fossa of pterygoid* (67).—Also in *Heloderma suspectum*, but not *H. horridum*; alternatively, *H. suspectum* and Varanidae may have acquired this condition separately.

W. *Vomers with distinct palatal shelves* (32).—The vomers are narrow, elongate structures only in *Heloderma* and *Varanus*, i.e., distinct palatal shelves are absent. Ancestrally, the vomers are broad as in *Lanthanotus borneensis*. However, in this species attainment of broad palatal shelves is probably a character reversal, judging from the narrow and elongate vomers exhibited by the late Cretaceous lanthanotine, *Cherminotus longifrons* (see Borsuk-Bialynicka 1984).

X. *Odontoid sutured and not fused to axis* (not listed, see Y).

Y. *Second intercentrum sutured and not fused to axis* (not listed).—The unfused odontoid and second intercentrum are size and age related characters (Gauthier 1982). These structures fuse to the axis in large, older individuals (e.g., *Varanus salvator* SDSNH 57080), as they do in all lepidosaurs.

This Paper:

Z. *Vomers more than twice as long as palatines* (31); *palatines approximately as wide as long* (33).—Although the form of the snout differs among these taxa, the vomers of helodermatids, and varanids are elongate, being nearly twice the length of the palatines. This condition is diagnostic of varanoids among anguimorphs, and among squamates generally. Elongate vomers may be associated with the transverse pterygopalatine suture, which has been interpreted as a functional response to over retraction of the hypokinetic axis (Borsuk-Bialynicka 1984). Concomitantly, the palatines and anterior ends of the pterygoids are shortened with respect to the vomers. In Recent *Heloderma* we note that the vomerine process of the palatine is further reduced such that it does not extend anteriorly beyond the level of the last maxillary tooth.

Elongate vomers also are characteristic of certain late Cretaceous anguimorphs from Mongolia shown in the plates and figures in Borsuk-Bialynicka (1984: figs. 2, 8, 11; plates 1, 5). They occur in *Gobiderma pulchrum*, perhaps *Paravaranus angusitfrons*, and *Proplatynotia longirostrata*. Thus, the character may be applicable at a taxonomic level more inclusive than Varanoidea, as constituted here.

AA. *Premaxillary teeth abruptly smaller than maxillary teeth* (23).

BB. *Supratemporal bone reaches level of parietal notch (apex of angle formed by*

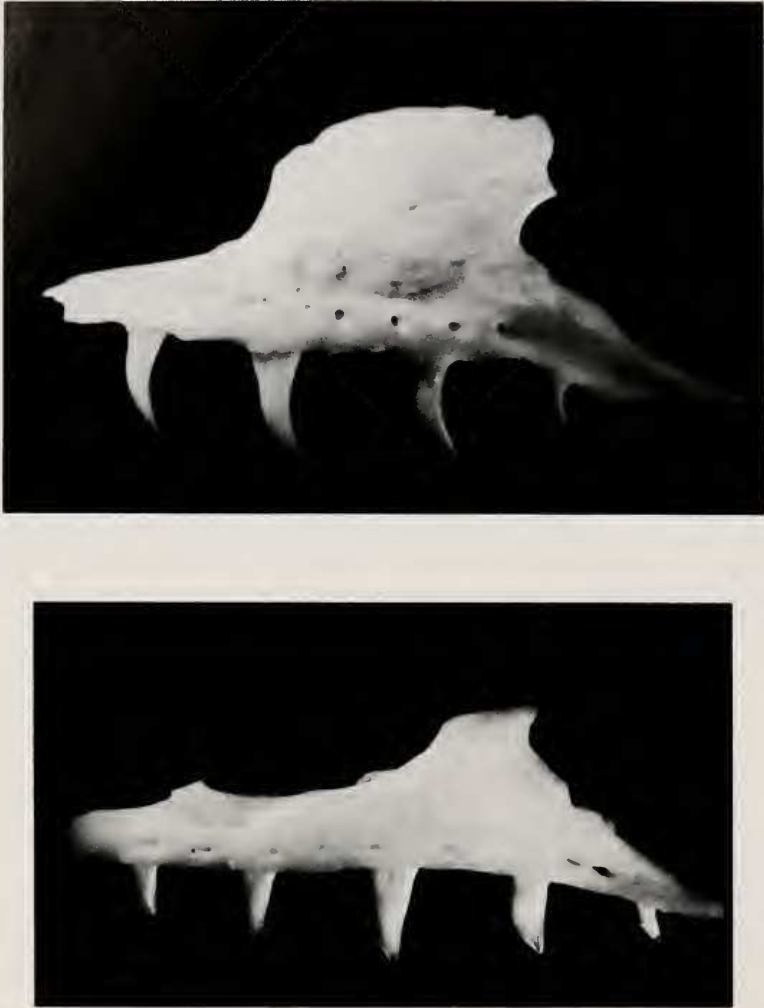


FIGURE 1. Lateral view of left maxilla of *Heloderma* (top) and *Varnaus* showing the derived, posterior position of the nasal process in the latter.

supratemporal processes) (19).—In varanoids the supratemporal is longer than in other Anguimorpha; it reaches anteriorly level with the apex of the parietal notch. This character may be associated with the 3b-layer of the MAME profundus (T, above), which takes its origin solely from this bone in varanoids, whereas in other anguimorphs it invades the descensus parietalis to varying degrees. Rieppel (1980a) considered that the varanoid condition of the muscle is primitive with respect to other squamates, although he used it as a diagnostic feature. Hence, a long supratemporal might also represent an ancestral condition. Our inspection of other anguimorphs brought mixed results; most have a short supratemporal relative to its distance from the parietal notch. Thus, the origin of the MAME profundus and the length of the supratemporal may be a synapomorphy of varanoids, and we believe that the consequent restriction of the MAME profundus to the supratemporal might therefore be a redundant character.

Synapomorphies of Varanidae (Varaninae + Lanthanotinae)

There are a number of characters within Varanoidea that designate varanines and lanthanotines as monophyletic and the sister group of helodermatids. Many of these

were first noted by McDowell and Bogert (1954). Rieppel (1980*a, b*) has reviewed the literature on alternative interpretations, favoring those with a phylogenetic emphasis. Based on head musculature (Rieppel 1980*a*) and the postcranial skeleton (Rieppel 1980*b*), he concluded, as have others before him, that *Lanthanotus* is phylogenetically closer to *Varanus* than it is to *Heloderma*.

The following is a compilation of characters shared between *Lanthanotus* and *Varanus* that have been considered derived; they are not found in *Heloderma*, or in squamates generally. The number in parentheses refers to the corresponding character(s) in Tables 2 and 3.

McDowell and Bogert (1954):

A. *Nasals fused* (1).—Borsuk-Bialynicka (1984) stated that the nasals might be paired in the early lanthanotine *Cherminotus*; however, photographs of the holotype (the best preserved specimen) reveal that the condition of the nasals cannot be determined with certainty.

B. *Fully retracted nares* (2, 4, and see F above).

C. *Nasal process of maxilla rises from a posterior position on that bone* (5). In helodermatids the nasal process of the maxilla is located in the middle of the maxilla (Fig. 1), the ancestral condition in anguimorphs. In *Varanus* and *Lanthanotus* the nasal process is positioned posteriorly as a result of elongation of the premaxillary process and reduction of the orbital process of the maxilla. This feature probably occurs in conjunction with fully retracted nares.

D. *Well-developed subolfactory processes directed posteromedially that closely approach one another, or contact midventrally* (9) (Fig. 2).

E. *Supraoccipital makes broad contact with parietal* (15).—Rieppel (1980*a*) further emphasized this synapomorphy. By contrast, Borsuk-Bialynicka (1984) regarded broad parietal contact as convergent, a response to reduced metakinesis in skulls of different proportions. Although possibly unrelated, we add (18) that the supratemporal processes of the parietal are very compressed mesolaterally in *Varanus* and *Lanthanotus*, and not so in other anguimorphs.

F. *Hypoglossal foramen enlarged, confluent with vagal foramen* (16).

G. *Double posterior lacrimal foramen* (22).—Two lacrimal ducts are present in *Heloderma*, *Lanthanotus*, and *Varanus* (P, above), whereas the duct is single in all other lepidosaurs (Gabe and Saint Girons 1976). There is, however, only a single posterior and anterior lacrimal foramen in *Heloderma*, but there are two posterior foramina in varanids. The anterior foramen is single in *Saniwa* and *Lanthanotus* (personal observation), and double in *Varanus*.

H. *Increased intramandibular kinesis* (37–45, and see C above).

I. *Osteoderms, when present, reduced, not fused to skull*. (48).

J. *Reduction of the outer conch of the quadrate* (20).

Hoffstetter and Gasc (1969):

K. *Nine cervical vertebrae* (49); *well-developed cervical and caudal peduncles* (53); *caudal chevrons do not contact centra condyles* (54).—Table 1 provides additional meristic data on the varanoid axial skeleton.

Lécuru (1968); Rieppel (1980*b*):

L. *Posterior coracoid emargination present* (57).—The presence of a posterior coracoid emargination is variable in *Lanthanotus*; see the conflicting descriptions of Lécuru (emargination absent) and Rieppel (present, but small). Our specimen of *Lanthanotus* is like Lécuru's in that no posterior coracoid emargination is present. It is also absent in *Saniwa* (personal observation).

M. *Fewer than four phalanges on pedal digit V* (not listed).—Rieppel (1980*b*) considered the loss of a phalanx in pedal digit V an apomorphic condition shared by

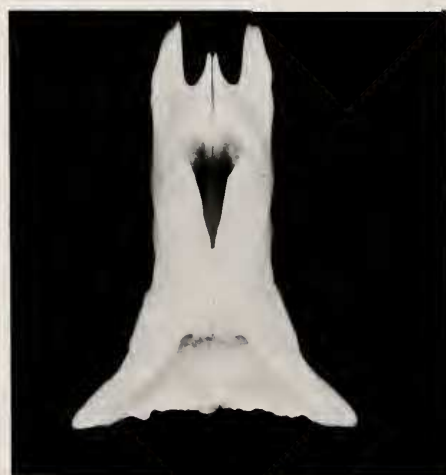


FIGURE 2. Frontal bones of *Heloderma* (top), *Lanthanotus* (middle), and *Varanus* (bottom). Ventral view (right) shows orientation of the subolfactory processes (anterior in *Heloderma*).

TABLE 1. Meristic characters of the varanoid axial skeleton.

	<i>Heloderma</i>	<i>Lanthanotus</i>	<i>Varanus</i>
No. cervical vert.	8	9	9
1st cervical rib	V4	V4	V5-7
No. presac. vert.	32-36	35	29
No. lumbar ribs	3-4	3	5
No. true lumbar vert.	2	1	1
No. caudal vert.	25-40	63-69	60-110
1st caudal chevron	V2 (3)	V2	V2

Heloderma and *Lanthanotus*. We confirm that only three phalanges are present in *Lanthanotus*, but all *H. suspectum* and at least some *H. horridum* at our disposal have the ancestral condition of four phalanges on the fifth pedal digit. Of seven *H. horridum* from the same brood born in the Detroit Zoo, four of these had four phalanges on the fifth pedal digit and three had three. We consider the variable number diagnostic of *H. horridum* among *Heloderma*.

Rieppel (1980a):

N. Articular socket present on dorsal surface of cephalic condyle of quadrate to receive squamosal peg (not listed).—We note the presence of this socket in large individuals of *Heloderma* and its absence in small *Varanus*. It may, therefore, be a size related character; more important, the peg and socket articulation appears to be a basic squamate character, as described by Robinson (1967).

O. *M. constrictor colli* extends anteriorly covering first ceratobranchials (63).

P. *M. genioglossus lateralis* subdivided into separate bundles (66).

Q. Anterior head of *M. pseudotemporalis profundus* enlarged (68).

Branch (1982):

R. Hemipeneal morphology, viz., paired horns develop as extensions of the main retractor muscle (70).—In a recent examination of cloacal and hemipenial musculature of lizards, Arnold (1984), not citing Branch (1982), described a combination of derived characteristics for Varaninae. He (Arnold 1984:75) concluded, "but, as these are not shared with the other two surviving platynotan families, which approach the generalized lizard condition, they provide no evidence of relationships among these groups." Arnold's assessment may not be in contradiction of Branch (1982), who apparently was referring to cartilage-like conical horns penetrating the hemipenial lumen in *Lanthanotus* and *Varanus*. We retain this character as a synapomorphy of Varanidae.

Gauthier (1982):

S. Surangular does not extend anteriorly far beyond coronoid eminence (40).

T. Coronoid and surangular processes on posterolateral margin of dentary reduced (38).

U. Intramandibular septum without posteroventral notch (41).

V. Splenial moves with dentary (44).

Schwenk (MS):

W. Foretongue notched for at least 40% of length (72).

Estes, de Queiroz, and Gauthier (MS):

X. Second epibranchial absent (77).

Y. Three or fewer pairs of sternal rib attachments (61).

Convergent Characters within Varanoidea

Monophyly of Varanoidea, composed of Helodermatidae, Lanthanotinae and Varaninae, is supported by 37 synapomorphies (Tables 2 and 3); 26 others unite Lanthanotinae and Varaninae as Varanidae, the sister group of Helodermatidae (Fig. 3). Helodermatidae is diagnosed by 23 characters (*see* Part II). Several derived characters, therefore, must be regarded as convergent acquisitions between *Lanthanotus* and *Heloderma*.

Heloderma and *Lanthanotus* are convergent in the following nine derived characters: frontals trapezoidal (6); prefrontal and postfrontal contact above the orbit (10); parietal foramen absent (11); absence of upper temporal bar (12 and 13); rounded snout (21); and more than 30 presacral vertebrae (51). Estes et al. (MS) also note that *Lanthanotus* and *Heloderma* have acquired independently the absence of an ossified palpebral (78), and a reduced number of scleral ossicles (79).

Convergence in the skull characters is revealed by the early lanthanotine *Cherminotus longifrons* Borsuk-Bialynicka, which retains the ancestral conditions of some of these characters (e.g., characters 6, 10, 11, 12, and 21) by comparison to *Lanthanotus* and *Heloderma*. Moreover, unlike *Lanthanotus*, in *Cherminotus* the parietals are not elongate nor are the frontals foreshortened; the splenial is not as short posteriorly; and the vomers are narrow. However, it can be identified as a lanthanotine by details of skull morphology, in addition to those characters above that *Lanthanotus* shares (convergently) with *Heloderma*. *Cherminotus* also shares apomorphies with varanines, such as external nares that are nearly completely retracted, broad contact of the supraoccipital with the parietal, and the absence of fused cephalic osteoderms.

Discussion of Varanoidea

Operationally, Varanoidea needs to be placed in a framework with necrosaurids and other extinct "platynotans." Unfortunately, the state of preservation of most necrosaurian taxa is insufficient for more than a provisional diagnosis of the group. Moreover, necrosaurids are characterized primarily by ancestral features. Although they display some unusual combinations of ancestral anguimorph and varanoid characters, only the condition of fused frontal bones in some adult necrosaurids could be considered diagnostic. The shape of the parietal, maxilla and teeth, as well as features of the mandible indicating limited kinesis, suggest that these early and generalized anguimorphs are related to varanoids. However, necrosaurids lack well-developed subolfactory processes below the frontals, at least in the better preserved specimens. Likewise, the external nares are only weakly retracted, and in some there is only incipient infolding of the tooth bases (Borsuk-Bialynicka 1984, Estes 1983a). Osteoscutes may be rhomboid, polygonal or oval, fused to the skull roof or free (Estes 1983). At this time, necrosaurids, as Estes (1983) hypothesized, are probably best understood as being a collection of fairly generalized platynotans.

Borsuk-Bialynicka (1984) has evaluated Platynota in the context of a polyphyletic origin from various members of a "necrosaurian stock." She recognized a polyphyletic grade "modern Platynota" that consists of Varanidae, Lanthanotidae, Helodermatidae and Mosasauridae. This group is identified by those classical characters used by previous workers: 1) a high degree of intramandibular kinesis (less so in Helodermatidae); 2) strong development of the subolfactory processes (not in Mosasauridae); 3) teeth with prominent basal infolding (less so in Helodermatidae); 4) a transverse pterygopalatine suture; 5) retracted external nares (only incipient in Helodermatidae); 6) size increase; 7) fragmentation of cephalic osteoderms (unknown in mosasaurs).

Borsuk-Bialynicka (1984) argued from functional considerations of the skull, especially with regard to gradual improvement of predatory adaptations (such as modifications of the palatal elements). In her scheme, helodermatids were independently derived, and even lanthanotines and varanines were regarded as clades that originated separately from "necrosaurs." The host of derived osteological features shared by

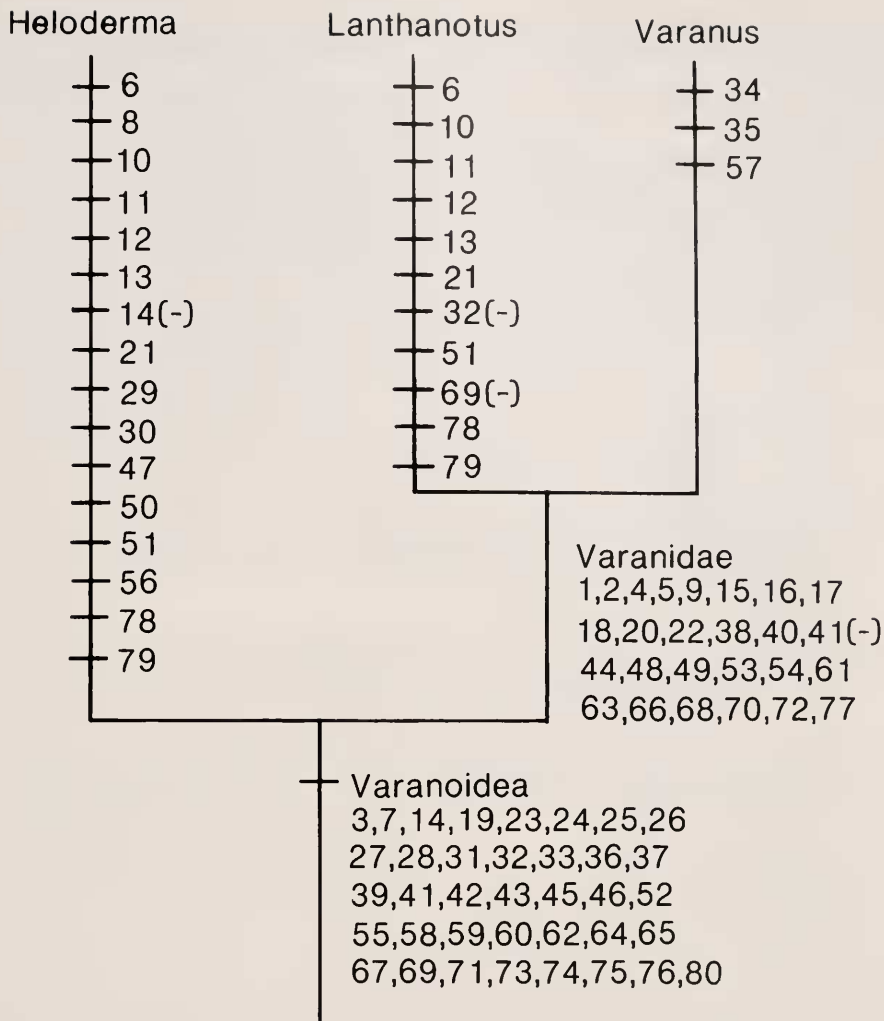


FIGURE 3. The relationships of Varanoidea as determined from character states in Tables 2 and 3. [PAUP: 93 steps, C.I. = 0.86]

varanines and lanthanotines (*see above*) are believed by Borsuk-Bialynicka to be parallel achievements, a conclusion with which we strongly disagree. For example, she believed that the broad contact of the supraoccipital with the parietal was a convergent means of restricting metakinetic movement, which itself was a response to overall proportions of the brain case and snout, these supposedly being different in the two taxa.

We conclude that monophyly of Recent varanoids and varanids are highly corroborated hypotheses. A phylogeny envisioning a polyphyletic origin implies only that considerable work remains to be done in character analysis of "Necrosauridae," Dolichosauridae, "Aigialosauridae" and Mosasauridae. It is safe to say that by the late Cretaceous Helodermatidae was represented by *Paraderma*, Lanthanotinae by *Cherminotus*, and Varaninae by *Saniwides* and *Telmasaurus* (Estes 1983a, Borsuk-Bialynicka 1984). For now, we are inclined towards a conservative interpretation, as suggested by Rieppel (1980a, b), that would recognize the monophyly of Varanoidea as a group restricted to Helodermatidae, Lanthanotinae and Varaninae. The name "Platynota" may be retained for convenience as it was applied by McDowell and Bogert, and by

TABLE 2. Character summary of Varanoidea, arranged in anatomical sequence, and scored as ancestral (0) or derived (1). Those preceded by "v" are diagnostic of Varanoidea. See Table 3 for character state distribution.

Skull characters

1. Nasal bones paired (0), or fused (1).
2. Nasal and prefrontal bones in broad contact (0), or with little or no contact (1).
- 3.v Nasal and maxillary bones in broad contact (0), or with little or no contact (1).
4. Nasals and maxillary bones in narrow contact (0), or not in contact (1).
5. Nasal process of maxilla rises from the middle (0), or posterior (1) aspect of maxillary.
6. Frontal more or less parallel-sided (0), or trapezoidal (1).
- 7.v Subolfactory processes of frontals short, not in contact ventromedially (0), or well-developed and closely opposed or contacting ventromedially (1).
8. Subolfactory processes of frontals do not descend to contact each other anteromedially (0), or do so (1).
9. Subolfactory processes of frontal do not descend to approach or contact each other posteromedially (0), or do so (1).
10. Prefrontal does not (0), or does closely approach or contact postfrontal above orbit (1).
11. Parietal foramen present (0), or absent (1).
12. Postorbital present (0), or absent (1).
13. Squamosal large, extending to postorbital (0), or small and reduced (1).
- 14.v Temporal musculature inserts ventrally (0), or dorsally (1) on parietal table.
15. Supraoccipital not in broad contact with parietal (0), or with broad contact (1).
16. Hypoglossal foramen not enlarged (0), or enlarged (confluent with vagal foramen) (1).
17. Carotid duct present (0), or absent (1).
18. Supratemporal process of parietal broad in dorsal aspect (0), or narrow (1).
- 19.v Supratemporal bone does not reach level of apex of parietal notch (0), or does (1).
20. Quadrate with large outer conch (0), or conch reduced (1).
21. Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1).
22. Posterior lacrimal foramen single (0), or double (1).
- 23.v Premaxillary teeth large (0), or abruptly smaller than maxillary teeth (1).
- 24.v Plicidentine teeth absent (0), or present (1).
- 25.v Teeth bluntly pointed (0), or sharply pointed, trenchant, recurved, and widely-spaced (1).
- 26.v Successional replacement teeth in resorption pits (0), or replacement teeth develop posteriorly, no resorption pits present (1).
- 27.v Maxillary tooth row extends posteriorly of orbit (0), or is entirely antorbital (1).
- 28.v Maxillary teeth number 13 or more (0), or less than 13 (1).
29. Maxillary teeth greater than 9 (0), or less than/equal 9 (1).
30. Venom groove absent (0), or present (1).
- 31.v Vomer short (0), or nearly twice the length of palatine (1).
- 32.v Palatal shelves of vomer wide (0), or narrow (1).
- 33.v Palatine longer than wide (0), or equally wide as long (1).
34. Palatine teeth present (0), or absent (1).
35. Pterygoid teeth present (0), or absent (1).
- 36.v Ectopterygoid does not contact palatine anteriorly (0), or does to exclude maxilla from suborbital fenestra (1).
- 37.v Dentary and surangular overlap considerably (0), or very little (1).
38. Coronoid and surangular processes of dentary well-developed (0), or processes reduced (1).
- 39.v Surangular tapered anteriorly (0), or blunt and expanded anterodorsally (1).
40. Surangular extends well beyond coronoid eminence (0), or does not (1).
- 41.v Inramandibular septum (IMS) without posteroventral notch (0), or notched (1).
- 42.v Splenial extends posterior of coronoid eminence (0), or does not (1).
- 43.v Splenial-dentary suture firm (0), or loose, with much connective tissue between the two bones (1).
44. Splenial does not move with dentary (0), or does (1).
- 45.v Coronoid without long anterolateral and anteromedial processes (0), or processes present (1).
- 46.v Head scales large and plate-like (0), or partly or completely fragmented (1).
47. Osteoderms thin, plate-like (0), or rounded and thick (1).
48. Osteoderms fused to skull (0), or not (1).

Axial characters

49. Number of cervical vertebrae eight (0), or nine (1).
50. Vertebral centra long and neural spines broad (0), or centra short and neural spines narrow and tall (1).
51. Number of presacral vertebrae fewer than 30 (0), or more (1).
- 52.v Caudal vertebrae autotomic (0), or not (1).
53. Peduncles on cervical and caudal vertebrae short (0), or long (1).
54. Caudal chevrons and cervical hypapophyses (=intercentra) contact centrum condyle (0), or on centrum only (1).

TABLE 2. Continued.

Appendicular characters

- 55.v Epicoracoid contacts suprascapula and mesoscapula (0), or not (1).
 56. Anterior coracoid emargination present (0), or absent (1).
 57. Posterior coracoid emargination absent (0), or present (1).
 58.v Clavicle loop-shaped medially (0), or gracile and not expanded (1).
 59.v Interclavicle with long anterior process (0), or process short or absent (1).
 60.v Mesosternum present (0), or absent (1).
 61. Rib attachments on sternum more than three pairs (0), or three or fewer pairs (1).

Myological characters

- 62.v M. episterno-cleido-mastoideus does not reach parietal (0), or has extensive insertion on parietal (1).
 63. M. constrictor colli does not cover 1st ceratobranchials (0), or does (1).
 64.v Origin of MAME profundus from supratemporal and parietal (0), or supratemporal only (1) [may be redundant with 19, see text].
 65.v Insertion of M. geniomyoideus is completely superficial to M. genioglossus medialis (0), or insertion is at least partly deep to M. genioglossus medialis (1).
 66. M. genioglossus lateralis single (0), or subdivided into separate bundles (1).
 67.v? Insertion of M. levator pterygoidii extends posteriorly beyond columellar fossa of pterygoid (0), or does not (1).
 68. Anterior head of M. pseudotemporalis profundus not enlarged (0), or enlarged (1).
 69.v? Bodenaponeurosis with broad base (0), or narrow base attached only to caudomesial edge of coronoid (1).

Other characters

70. Hemipenis without paired horns as extensions of main retractor muscles (0), or with them (1).
 71.v Foretongue not deeply cleft (0), or deeply cleft (not less than 20% of length) (1).
 72. Foretongue cleft for 20% of length or less (0), or not less than 40% of length (1).
 73.v Gland of Gabe absent (0), or present (1).
 74.v Calyciform duodenal cells simple (0), or sero-mucous type (1).
 75.v Cochlear duct not robust (0), or robust and broad, limbus elongate and heavy (1).
 76.v Ulnar nerve superficial (0), or deep (1) in forearm.
 77. Second epibranchial present (0), or absent.
 78. Ossified palpebrals present (0), or absent (1).
 79. Scleral ossicles 14 (0), or fewer (1).
 80.v Lacrimal duct single (0), or double (1).
-

Rieppel, but with the understanding that the monophyly of that group has not yet been established.

II. SYSTEMATIC ACCOUNT OF HELODERMATIDAE

In this section we describe new fossils of helodermatids, and provide a systematic review of the taxa assigned. Our decisions on character state polarity are based on the foregoing assessment of varanoid characters and relationships.

Amniota
 Squamata
 Autarchoglossa
 Anguimorpha
 Varanoidea
 Helodermatidae
Lowesaurus, new taxon
 Figures 4–6

Type species.—*Heloderma matthewi* Gilmore, 1928.

Diagnosis.—A taxon distinct from other Helodermatidae in possessing triangular frontal bones, as opposed to trapezoidal.

Etymology.—The name honors Charles H. Lowe, Professor of Biological Sciences at the University of Arizona, in recognition of his extensive contributions to the ecology of western North America.

TABLE 3. Distribution of varanoid character states from Table 2 (1 = derived, 0 = ancestral, 9 = missing data); a phylogeny is shown as Fig. 3.

	"Necrosauridae"	<i>Heloderma</i>	<i>Lanthanotus</i>	<i>Varanus</i>
Character:				
1.	0	0	1	1
2.	0	0	1	1
3.	0	1	1	1
4.	0	0	1	1
5.	0/1	0	1	1
6.	0	1	1	0
7.	0	1	1	1
8.	0	1	0	0
9.	0	0	1	1
10.	0	1	1	0
11.	0	1	1	0
12.	9/0	1	1	0
13.	9/0	1	1	0
14.	1	0	1	1
15.	0	0	1	1
16.	9	0	1	1
17.	9	0	1	1
18.	0	0	1	1
19.	9	1	1	1
20.	9	0	1	1
21.	0	1	1	0
22.	9	0	1	1
23.	1	1	1	1
24.	1/0	1	1	1
25.	1	1	1	1
26.	0/1	1	1	1
27.	1/0	1	1	1
28.	0	1	1	1
29.	0	1	0	0
30.	0	1	0	0
31.	1	1	1	1
32.	1	1/9	0	1
33.	0	1	1	1
34.	0	0	0	1
35.	0	0	0	1
36.	0/1	1	1	1
37.	9	1	1	1
38.	0	0	1	1
39.	9	1	1	1
40.	0	0	1	1
41.	1	1/0	0	0
42.	1	1	1	1
43.	9	1	1	1
44.	9	0	1	1
45.	1	1	1	1
46.	1	1	1	1
47.	0	1	0	0
48.	0/1	0	1	1
49.	9	0	1	1
50.	0	1	0	0
51.	0	1	1	0
52.	9	1	1	1
53.	9	0	1	1
54.	0?	0	1	1
55.	9	1	1	1
56.	9	1	0	0
57.	9	0	0	1
58.	9	1	1	1
59.	9	9	1?	1
60.	9	1	1	1
61.	9	0	1	1

TABLE 3. Continued.

	"Necrosauridae"	<i>Heloderma</i>	<i>Lanthanotus</i>	<i>Varanus</i>
62.	9	1	1	1
63.	9	0	1	1
64.	9	0	0	0
65.	9	1	0	1
66.	9	0	1	1
67.	9	1/0	1	1
68.	9	0	1	1
69.	9	1	0	1
70.	9	0	1	1
71.	9	1	1	1
72.	9	0	1	1
73.	9	1	1	1
74.	9	1	1	1
75.	9	1	1	1
76.	9	1	1	1
77.	9	0	1	1
78.	0	1	1	0
79.	9	1	1	0
80.	9	1	1	1

Lowesaurus matthewi (Gilmore)

Synonym. — *Heloderma matthewi* Gilmore.

Holotype. — AMNH 990A, posterior part of left maxilla with three teeth.

Type locality. — Lewis Creek, Logan County, Colorado.

Previously referred specimens. — KUPV 7652, maxilla, Middle Oligocene, White River Formation, Logan Co., Colorado; UNSM 50011, partial skull represented by right maxilla, frontal, partial parietal, partial right jugal, right postfrontal, partial right pterygoid, partial right prefrontal, partial basisphenoid, supraoccipital, partial quadrate, isolated osteoscutes and a partial right dentary; Late Oligocene (Whitneyan), Brule Member, White River Formation, Morrill Co., Nebraska (Gilmore 1928, Yatkola 1976).

New material (this paper). — KUPV 49651, a nearly complete right frontal bone; KUPV 49652, two trunk vertebrae.

Locality and horizon (new material). — Redington Gap SW $\frac{1}{2}$, SE $\frac{1}{4}$, Sec. 14, T. 19n., R. 52W., 3 $\frac{1}{2}$ miles south and 9 $\frac{1}{2}$ miles west of Bridgeport, Morrill County, Nebraska. Mitchell Pass Member, Gering Formation, Arikaree group (early Miocene; approximately 25–27 mybp).

Description of new material. — The frontal bone (KUPV 49651) tapers anteriorly giving it a distinctive triangular outline (Fig. 4). It measures 16.6 mm and 7.8 mm along the medial and parietal borders, respectively. Articular surfaces for the pre- and postfrontal bones are clearly visible on the lateral margin, where they approach but not quite meet each other above the orbital rim. A scar marking the nasal overlap extends posterolaterally to the prefrontal suture. Dorsally, the bone is covered with polygonal osteoderms that presumably would have conformed to the shape of the epidermal scales. The osteoderms are irregular; they are shaped like flattened domes separated from one another by moderately deep grooves. Most have a granular texture, although the larger ones display tubercles and pits.

On the ventral surface, the robust subolfactory process is broken distally, and we cannot determine with certainty that it would have sutured midventrally with its counterpart from the left frontal, as happens in *Heloderma* (Fig. 2). The basal portion of the subolfactory process is concave and penetrated by two foramina at the center of the concavity.

Of the two referred vertebrae (KUPV 49652), one is missing the distal extent of each zygapophysis (Fig. 5). All that remains of the other is the centrum. The more

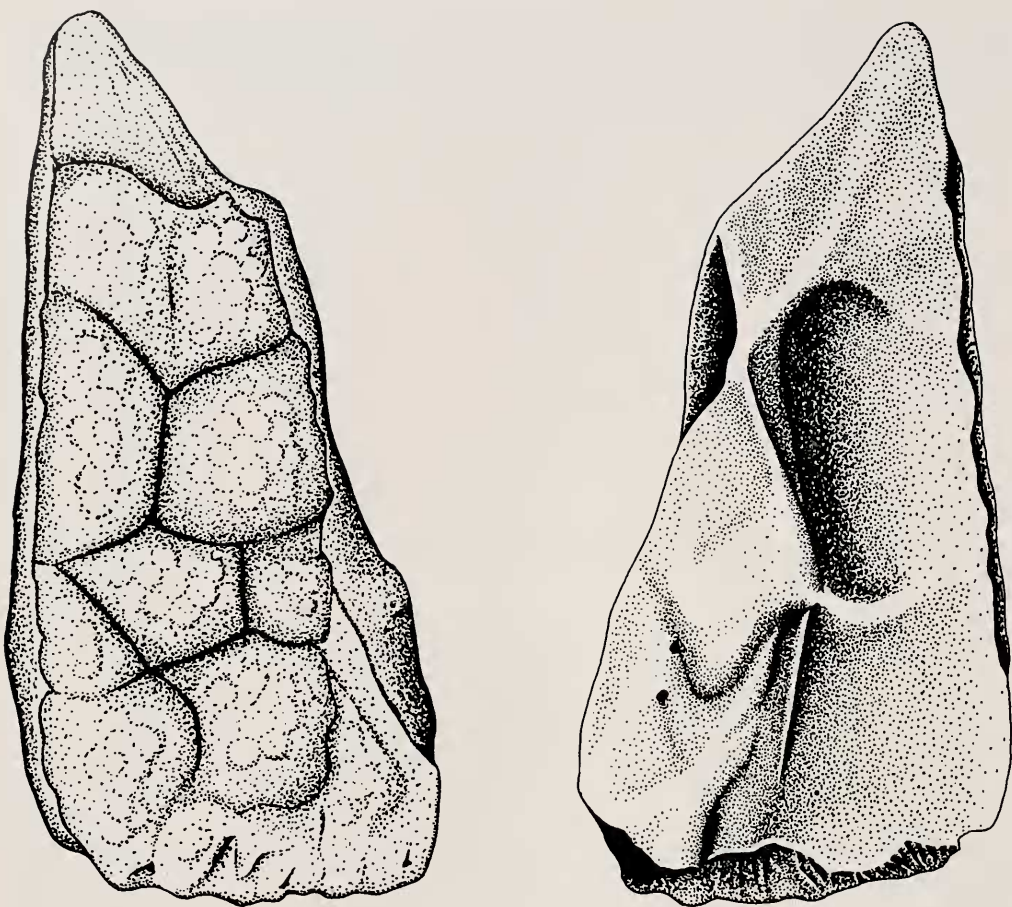


FIGURE 4. *Lowesaurus matthewi* (gen. nov.) right frontal (KUV 49651) drawn in dorsal (left) and ventral (right) views. Approx. $\times 7$.

complete specimen has a low, square profile not unlike characteristic trunk vertebrae of *Heloderma*. It is 5.8 mm from the inferior margin of the cotyla back to the tip of the condyle, and 7.8 mm across the tips of the prezygapophyses. The bone is 5.4 mm high measured from the posteroventral edge of the condyle to the top of the neural arch; the tip of the neural spine is missing. The lateral borders of the centrum are parallel, and the condyle is large, elliptical and preceded by a faint constriction. The neural arch is low and slopes gently posterodorsally.

Remarks. — Yatkola (1976:6) illustrated a complete frontal bone articulating with a partial parietal (UNSM 50011), as part of the material that he referred to *H. matthewi*. Reexamination of this fossil (Fig. 6) and comparison with KUV 49651 in hand shows them to be similar in overall shape, position of the articular facets, and robustness of the subolfactory processes. KUV 49651 differs in having slightly larger, higher and more tuberculate osteoderms separated by deeper grooves. Certainly the most compelling feature in common is their triangular shape.

Ancestrally, the frontal bones of anguimorphs are parallel-sided above the orbits and laterally expanded at the anterior and especially posterior ends; the frontal participates broadly in the orbital rim (Gauthier 1982). In helodermatids ancestrally, the frontals are trapezoidal, broad above the orbits, and with very little (*Lowesaurus*) or no (*Heloderma*) participation in the orbital rim owing to the contact of the pre- and postfrontal bones. Also important is that the descending subolfactory processes suture anteromedially. The triangular frontals of *Lowesaurus* are thus unusual among anguimorphs, the shape being repeated elsewhere only in certain glyptosaurine anguids, for

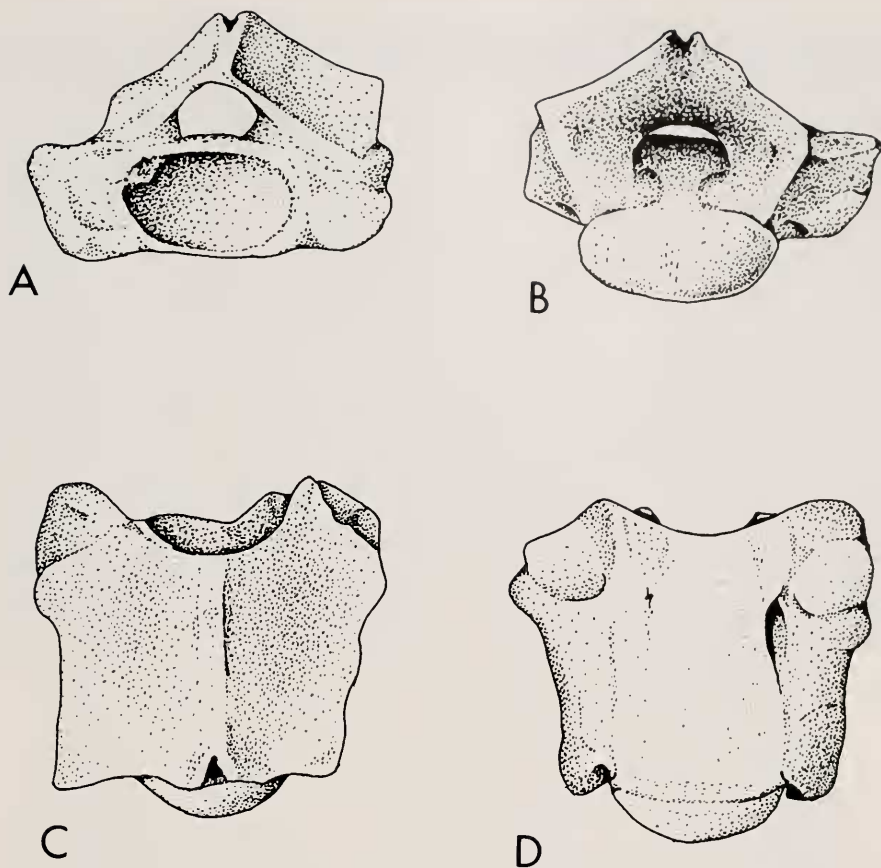


FIGURE 5. *Lowesaurus matthewi* (gen. nov.) vertebra (KUVP 49652) drawn in A) anterior, B) posterior, C) dorsal, and D) ventral views. Approx. $\times 7$.

example *Paraglyptosaurus princeps* (Sullivan 1979). In helodermatids, the direction of change in shape probably coincides with that seen within glyptosaurines, that is, from parallel-sided to trapezoidal to triangular. The frontals of *Paraderma bogerti* and *Eurheloderma gallicum* must be found in order to verify this hypothesis.

A New Helodermatid (Indet. Taxon) from the Latest Paleocene, Bighorn Basin, Wyoming

cf. *Eurheloderma*

Bartels (1983) recently described an isolated parietal (UMMP 74619) from the latest Paleocene of Wyoming (fig. 5; p. 367). He referred to this specimen as a varanoid of "indeterminate family, genus and species" (p. 367). Our examination of the specimen confirms that it is varanoid in that the supratemporal scar anteriorly extends to the level of the posterior end of the parietal table. Moreover, the absence of a parietal foramen and the insertion of the temporal musculature ventrally on the parietal table are derived characters diagnostic of Helodermatidae. The parietal table displays dermal rugosities, but the overlying osteoderms did not adhere (indicating a subadult individual) and were not preserved with the specimen. The parietal is constricted in the manner of *Eurheloderma* (see below), but assignment to that taxon would be premature in view of our uncertainty regarding the level at which this attribute appeared in helodermatid phylogeny. We list it *conferee Eurheloderma* merely to indicate the similarity. Beyond those diagnostic of Helodermatidae, the fossil reveals no other apomorphies, and we leave the taxon unnamed pending the discovery of additional material.



FIGURE 6. *Lowesaurus matthewi* (gen. nov). Dorsal (left) and ventral view (right) of frontal and partial parietal (UNSM 50011). Approx. $\times 3$.

Morphology of Helodermatidae

Our generic reassignment of the fossils previously referred to *Heloderma matthewi* implies that two lineages of helodermatid varanoids existed during the middle Tertiary of North America: *Lowesaurus* and *Heloderma* (represented by *H. texanum*, Fig. 7). Only the latter has persisted to the present. We also believe that *Paraderma bogerti* is an early helodermatid, which would thus extend the temporal range of the group back to the late Cretaceous in North America. Derived features discussed below are shared by all these taxa, at least where known.

Teeth and venom delivery.—The most unusual feature of helodermatids is their dentition. The anterior margin of each tooth is inflected medially to form a groove for the conduction of venom. The two living species *Heloderma suspectum* and *H. horridum* possess deeply infolded, well-developed venom grooves on the anteromedial margins of all maxillary and dentary teeth (Fig. 8), and frequently there are shallow grooves on the more lateral teeth of the premaxilla. The groove is best expressed on the largest teeth, those nearest the middle of the tooth row. In *Eurheloderma gallicum* and *Lowesaurus matthewi* the groove is not as pronounced as it is in the two Recent forms, but it does extend to the distal end of the tooth. The venom groove in *H. texanum* is similar to that in *E. gallicum* and *L. matthewi* except for having a wider basal opening as in the Recent species.

There are few teeth well preserved on the jaw elements referred to *Paraderma bogerti*. On the holotype (UCMP 54261; Fig. 9) the most complete tooth is near the middle of the dental row and bears an incipient groove on the anteromedial margin near the base. We can only speculate, however, that the groove is a venom-conducting precursor. The well-preserved premaxillary teeth of this lizard show no grooves, but weakly grooved premaxillary teeth occur only in living helodermatid species.

In fossils of the early varanoids *Palaeosaniwa canadensis*, *Parasaniwa wyomingensis*, *Provaranosaurus acutus*, and *Necrosaurus cayluxi* the trenchant margins of the teeth are distinctly delimited from the main shaft of the tooth, leaving what could also be interpreted as a precursor of a venom conducting groove. Here it is of interest that

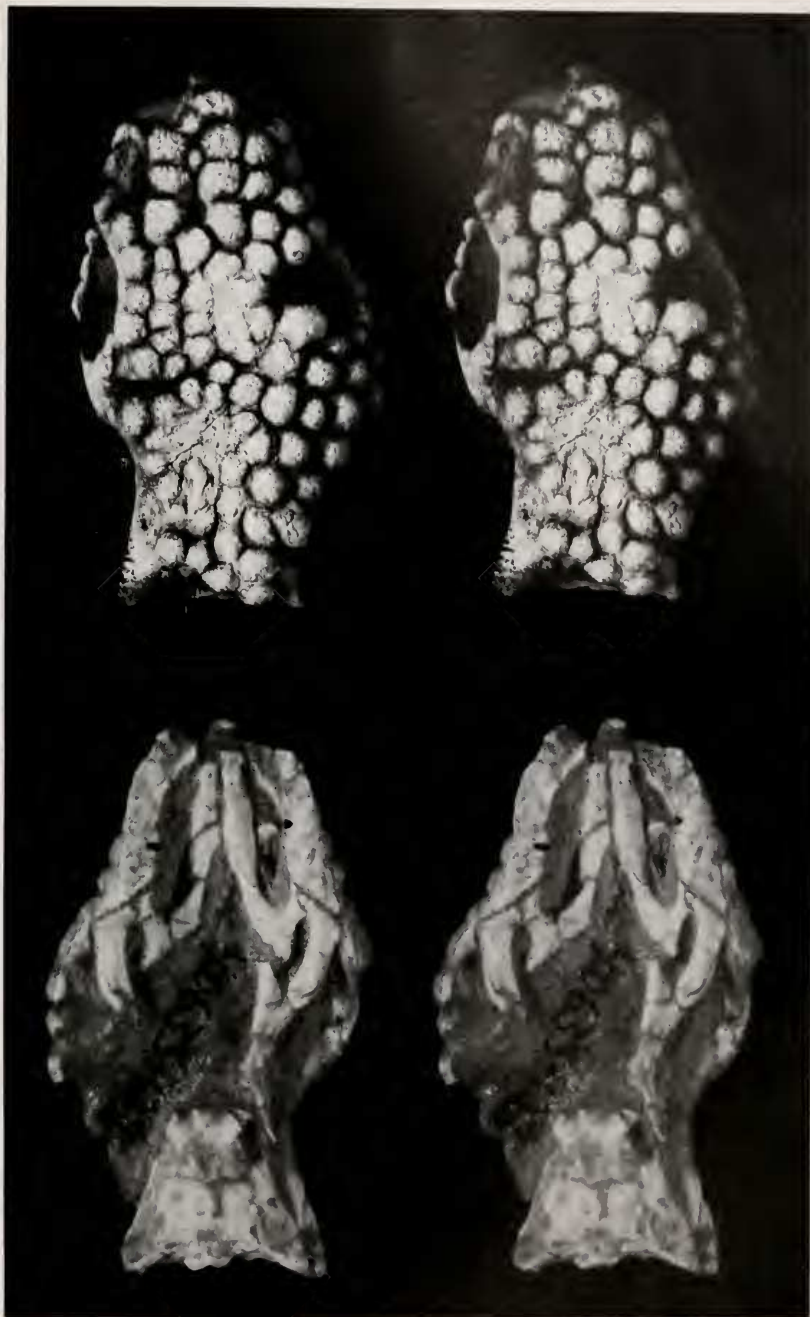


FIGURE 7. Stereopairs of *Heloderma texanum* Stevens (holotype UT 40635-123); skull in dorsal (top) and ventral views (bottom). Approx. $\times 2$.

Saint Girons (1977) and Kochva (1974) noted the presence of a large sero-mucous gland on the lower jaw of all varanoids, the Gland of Gabe, which is the venom producing organ in *Heloderma*. Thus, it is not unlikely that the potential for venom delivery was present early in the history of varanoid lizards. The desert monitor of Pakistan, *Varanus griseus*, may itself produce toxic secretions according to Gorelov (1970), although Kochva (1978) has noted contradictory evidence. In any case, the

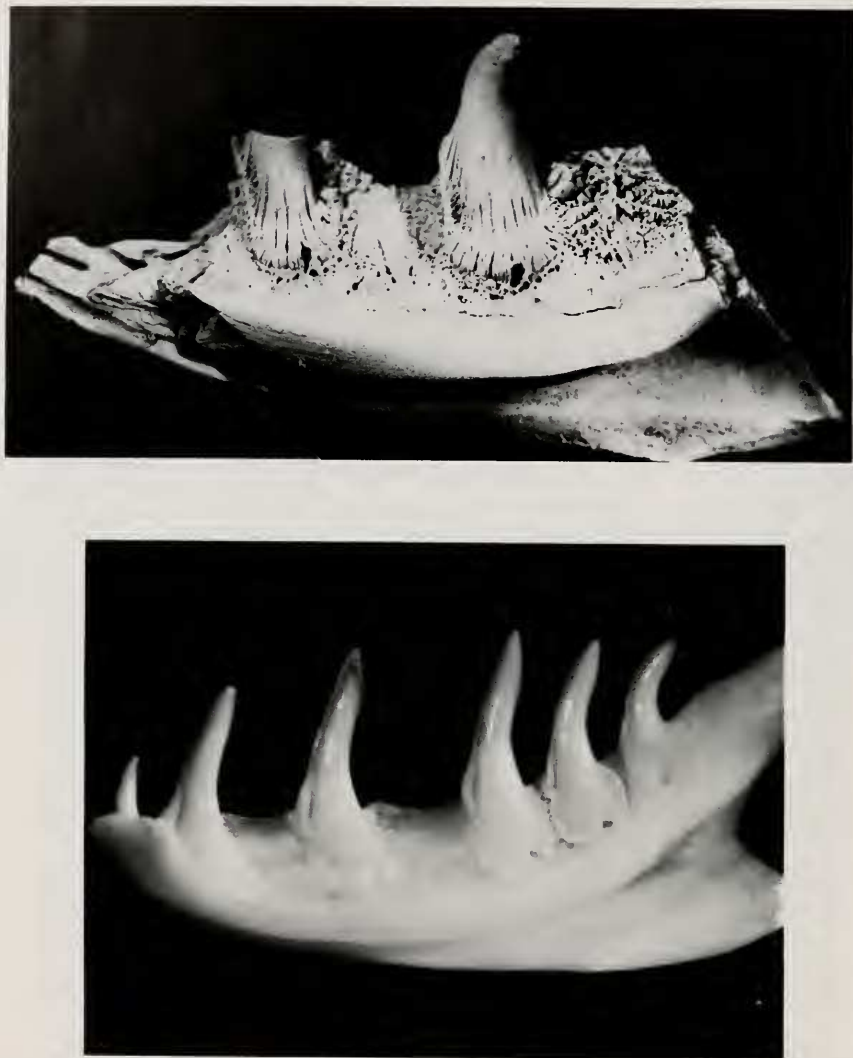


FIGURE 8. Right dentary of *Paraderma bogerti* (top, UCMP 49939; $\times 2$), and *Heloderma horridum* (bottom, SDSNH 59469; $\times 4.5$).

capability for venom injection was elaborated only within the more derived Helodermatidae, and as discussed in Part III, probably plays an important role in feeding.

Characteristic of varanoids, Helodermatidae have a reduced tooth count by comparison with other Anguimorpha. The number of teeth has decreased within helodermatid phylogeny as well. *Eurheloderma gallicum* has 11–12 maxillary teeth, and 12–13 dentary teeth. *Lowesaurus matthewi* has 11 teeth on the maxilla and *Heloderma texanum* has 9 (not 6 as reported by Stevens 1977). The dentary of *H. texanum* is unknown, and only a partial right dentary has been described for *Lowesaurus* (Yatkola 1977). Of the two Recent species, *H. horridum* is thought to possess the fewest number of maxillary teeth: 6–7 as opposed to 8–9 in *H. suspectum* (McDowell and Bogert 1954, Bogert and Martín del Campo 1956, Yatkola 1976). Our sample ($n = 80$) of skeletons confirms this only incidentally; the overlap in tooth count is in fact considerable. The maxillary tooth count of *H. horridum* varies from 6–9 with a mean and mode of 7. In *H. suspectum* the range is 7–9 with a mean and mode of 8. In both species, approximately one-third of our sample included individuals with a one-tooth count difference between left and right jaws.

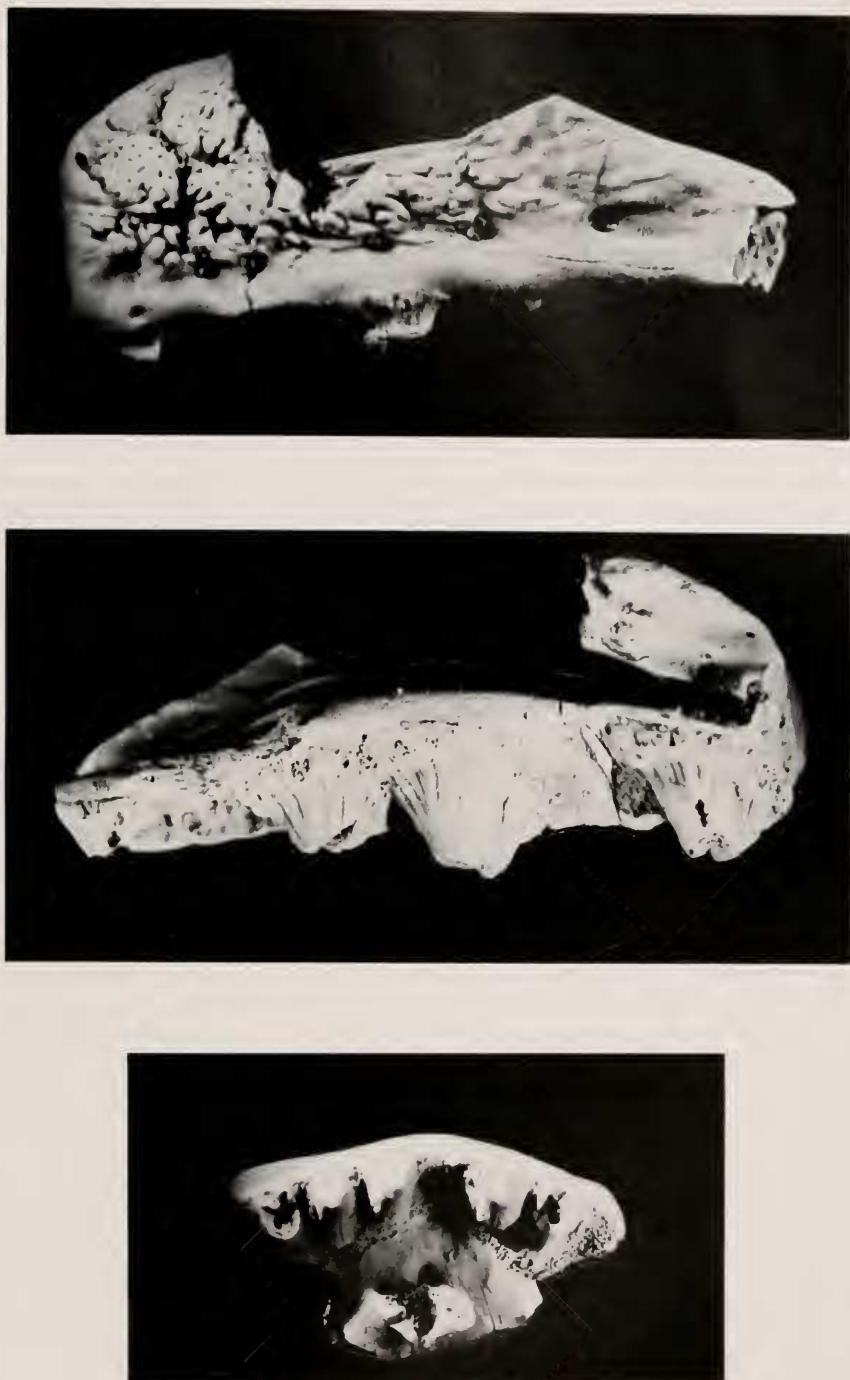


FIGURE 9. *Paraderma bogerti*. Maxilla (holotype UCMP 54261) in lateral (top) and medial (middle) views; premaxilla (bottom, UCMP 54199). Approx. $\times 3$.

The mean and mode of dentary teeth for both species samples is 9. *Heloderma horridum* varies from 8–10, and all individuals of *H. suspectum* examined had 9 dentary teeth except for one, which had 10 teeth on one jaw and 11 on the other.

Maxillary arch.—The maxillary arch of helodermatids is similar to both *Lan-*

thanotus and *Varanus* in that the tooth row is entirely antorbital, a feature emphasized by McDowell and Bogert (1954) to distinguish Varanoidea from other Anguimorpha (see above). A consequence of the antorbital tooth row in varanoids is that the palatine and ectopterygoid contact one another distally to exclude the supradental shelf from participating in the suborbital fenestra. This condition is evident in *H. texanum* and appears also to be the case in *Eurheloderma* and *Lowsaurus*, to judge from the palatine and ectopterygoid articular surfaces on the fossil maxillae. It was probably also the case for *Paraderma bogerti*, but more difficult to discern on this fossil.

Within Helodermatidae differences exist in the morphology of the maxilla. In the early forms *Paraderma*, *Eurheloderma*, and *Lowsaurus*, the dental shelf, indeed the entire maxilla, is deeply curved medially. The shelf is essentially straight in *Varanus* and *Lanthanotus*. In *Heloderma texanum* the shelf is rather narrow and straight (Fig. 7), whereas in the two Recent species the shelf is also strongly curved. In these two, the anterior end of the shelf widens to form a cup-like depression that isolates the first 3 or 4 teeth. This depression is scarcely evident in *H. texanum*, and not at all in *Eurheloderma* or *Paraderma*.

Palate.—Teeth are present primitively on the palatal bones (vomer, palatine, pterygoid) of diapsid amniotes. In general, lepidosaurs have retained palatal dentition throughout their evolution, but reduction and loss have occurred independently several times, particularly within squamates. Consequently, the absence of palatal teeth is a character often difficult to resolve phylogenetically. Within squamates, the loss of palatal teeth proceeds from the vomer to the palatine to the pterygoid (Camp 1923, Estes et al. MS). Neither modern species of *Heloderma* retains teeth on the vomer, but in contrast to previous reports, teeth may be present or absent on one or both of the pterygoids and palatines. On the holotype of *H. texanum*, a few small teeth are present on the palatine, but not on the pterygoid as reported by Stevens (1977). This condition is aberrant and may be peculiar to that specimen, or an artifact of preparation or fossilization.

A primitive feature of the palatine of *H. texanum* is that the vomerine process extends anteriorly beyond the level of the penultimate tooth of the maxilla, where it articulates with the vomer. This condition also occurs in Varanoidea. The derived palatovomer articulation is posterior to the level of the last maxillary tooth, as in living *Heloderma*.

Jugal.—The angle formed by the dorsal and anterior processes of the jugal is less acute in *Heloderma texanum* than it is in *H. suspectum* and *H. horridum*. The deflection is like that of other anguimorphs, such that the orbits are more oval than round and contribute to a lower profile of the skull. The low skull profile of *H. texanum* could be the result of allometry, i.e., the holotype specimen being a subadult (see below). A partial right jugal is known for *Lowsaurus* (UNSM 50011), but it is too incomplete to reconstruct accurately the shape of the orbit.

Parietal.—In helodermatids the parietal is flat and the adductors take their origin from the ventral surface, a derived condition among Varanoidea. The parietal of *Lowsaurus* and *Heloderma* is broad and trapezoidal, a shape common to all anguimorphs. The parietal of *Paraderma bogerti* is unknown. That of *Eurheloderma gallicum* is markedly constricted just anterior to the diverging supratemporal processes, as in UMMP 74619 described above. Yatkola (1976) considered this to be a derived condition, which may be correct, but the parietal of *Paraderma* must be found to verify the polarity.

Cephalic osteoderma.—Autarchoglossans primitively have large, plate-like dorsal scales that grade into smaller scales anteriorly and laterally. Varanoids are distinguished from other anguimorphs by the fragmentation of the large scales and osteoderms on the frontal and parietal, except for those of *Parasaniwa wyomingensis* and *Palaeosaniwa canadensis*, which are like those of anguimorphs ancestrally (Estes 1964, 1983a).

As characters, osteoderm size and surface texture are difficult to interpret and score. Descriptions are likely to be subjective, and the structures themselves probably

vary individually, with position on the skull, and ontogenetically. The dilemma is that there are precious few other features with which to evaluate many of the fossil taxa.

In helodermatids the parietal osteoderms are largest in *Eurheloderma gallicum*, smaller in *Lowesaurus matthewi*, smaller still in *Heloderma texanum*, and smallest in *H. suspectum* and *H. horridum*. The maxillary osteoderms are larger than those on the frontal in *E. gallicum*, *L. matthewi* and *H. texanum*, but approximately equal in size in *H. suspectum* and *H. horridum*.

Within helodermatids, the grooves between adjacent osteoderms deepen with fragmentation and thickening of the osteoderms themselves. They are shallow in *P. bogerti*, *E. gallicum*, and *L. matthewi*, deep in *H. texanum*, and deeper yet in *H. suspectum* and *H. horridum*. Finally, the surface of the osteoderms is simply vermiculate in *P. bogerti* and *E. gallicum*, whereas in *L. matthewi* the surface is mostly vermiculate but with tubercles on the largest osteoderms. The osteoderms of *H. texanum* are mostly tuberculate, and pitted and tuberculate in *H. suspectum* and *H. horridum*.

Vertebrae.—The vertebrae of *Paraderma bogerti* are unknown, and, except for a more constricted vertebral canal, there is little to distinguish those of *Lowesaurus matthewi* from the vertebrae of *Eurheloderma gallicum* figured by Hoffstetter (1957: 784). Estes (1963) illustrated a vertebrae from the early Miocene Thomas Farm locality of Florida and described it as *Heloderma*-like, although he referred it to Anguidae; subsequently it was placed provisionally with helodermatids (Estes 1983a). By comparison to the Florida specimen, the KUVF vertebra of *L. matthewi* is half as large, and the centrum is not compressed laterally. The vertebra of *L. matthewi* is larger than that of *H. texanum*, which also has a laterally compressed centrum.

In *Heloderma* the trunk vertebrae are short relative to those of *Lanthanotus* and *Varanus*, and the neural spines are narrower and more acute. There is a modest increase in the centrum length of posterior vertebrae of *Heloderma*, *Lanthanotus*, and squamates generally. Yet, in *Varanus* the vertebral centra tend to increase in length towards the anterior trunk region.

Body size.—The modern species of *Heloderma* are larger than their Tertiary relatives, assuming that the fossils represent adults of near average maximum size. However, for most of the fossil material none of the reliable signs of adulthood and maximum size, such as fusion of the epiphyses, basicranial elements, and girdles, are known.

Stevens (1977) suggested that the relative degree of fusion of osteoderms to the skull of *H. texanum* indicated that the holotype represents an adult. More important to us are the unfused sutures on the basicranium and low skull profile, both characteristic of a subadult individual. In *H. suspectum* and *H. horridum* the head tends to become broader in proportion to its length during growth, especially in males (Bogert and Martín del Campo 1956). That being the case, allometry may explain the wide angle of the jugal and comparatively elongate skull of the *H. texanum* holotype. We would estimate the snout-vent length of that individual at approximately 180 mm, and that of the other fossil helodermatids at no more than 250 mm, except one specimen (UCMP 49939) that may represent *P. bogerti*, which was at least 800 mm by extrapolation from the mandible of Recent *Heloderma*.

Bogert and Martín del Campo (1956) listed the average maximum snout-vent lengths of *H. suspectum* and *H. horridum* at 325 mm and 350 mm, respectively. However, two UMMZ specimens of *H. horridum* are considerably larger (♂ 382 mm SVL, ♀ 421 mm SVL), and neither specimen displays all the developmental characteristics marking cessation of growth. Our sample of skeletons indicates that the disparity in size between the smaller *H. suspectum* and the larger *H. horridum* is considerably greater than Bogert and Martín del Campo (1956) thought.

Other characters.—The two living species of *Heloderma* differ from one another in several ways (see part III). The most obvious of these is the proportionately longer tail of *H. horridum*. Bogert and Martín del Campo (1956) noted this difference and isolated several characters of this condition: in *H. horridum* the tail comprises at least 65 per cent of the snout-vent length; there are 40 instead of 25 to 28 caudal vertebrae;

and at least 75 rows of subcaudal scales instead of no more than 62. A relatively long tail is ancestral among Anguimorpha (see Part III).

The general color pattern of *H. horridum* is a mottled dark dorsum and banded tail; perhaps cryptic under some circumstances, this pattern is widespread among anguimorph lizards (e.g., Anguidae such as *Gerrhonotus*, the xenosaurs, and varanids such as *V. tristis*). The more brightly marked, pink and black pattern of *H. suspectum* is derived, perhaps serving biological roles of camouflage, aposematism, or both (Bogert and Martín del Campo 1956; see also part III).

Finally, *Heloderma suspectum* retains the ancestral state of enlarged preanal scales, and four phalanges in pedal digit V.

Diagnosis of Helodermatidae

In a strict sense, a diagnosis is a list of a taxon's derived character states (autapomorphies). For Helodermatidae these are given below, and will distinguish this taxon from other varanoid lizards; additional descriptive, ancestral features are listed in the preceding accounts on varanoid characteristics.

Our diagnosis also is intended to serve as a means of hypothesizing intrafamilial relationships (Fig. 10). Obviously, we must make assumptions about the inclusion of referred fossil taxa in the absence of complete knowledge of their anatomy. None of these assumptions, however, is inviolate from the standpoint of available evidence. Helodermatidae is a taxon of varanoid Anguimorpha with the following attributes:

1. Osteoderms thick, hexagonal and covering the entire head and body as a "coat of mail."
2. Skull of robust construction having a steep nasal process of the maxilla, which contributes to a rounded muzzle and short face.
3. Parietal foramen absent.
4. Gland of Gabe elaborated as a venom producing organ, concomitant with grooved teeth on the maxilla and dentary; grooved teeth for venom delivery are best developed in the two living species.
5. Upper temporal arch lost through reduction of the squamosal and loss of postorbital (convergent in *Lanthanotus*).
6. Participation of frontal in orbit restricted, owing to approach (but not contact) of pre- and postfrontals along orbital margin.
7. Subolfactory processes of the frontal descending anteromedially, joining ventrally in a midline suture.
8. Maxillary dental shelf curved medially.
9. Palatines lacking deep choanal grooves (convergent in *Varanus*).
10. Palpebral ossification absent (convergent in *Lanthanotus*).
11. Pterygoid lappet of quadrate present.
12. Posterior opening of vidian canal at basisphenoid-prootic suture.
13. Splenial not extending anteriorly beyond tooth row midpoint.
14. Scleral ossicles fewer than 14.
15. Innervation of dorsal leg muscles by interosseous nerve [characters 10–15 from Estes et al. MS].
16. Vertebral neural spines narrow and tall, rising at an acute angle.
17. Hypapophyses on posterior cervicals reduced (Hoffstetter and Gasc 1969).
18. Body long (32–36 presacral vertebrae—Table 1).
19. Tail short (25–40 caudal vertebrae—Table 1).
20. Interclavicle simple, rod-shaped.
21. Anterior coracoid emargination absent.
22. Adductor musculature inserting on the ventral surface of the parietal table.
23. Diet includes unusually large prey items (see Part III).

Discussion of Helodermatidae

The phylogeny of Helodermatidae is depicted in Figure 10 (Table 4); it is nearly free of homoplasy (convergence and reversals) and describes a fairly unambiguous

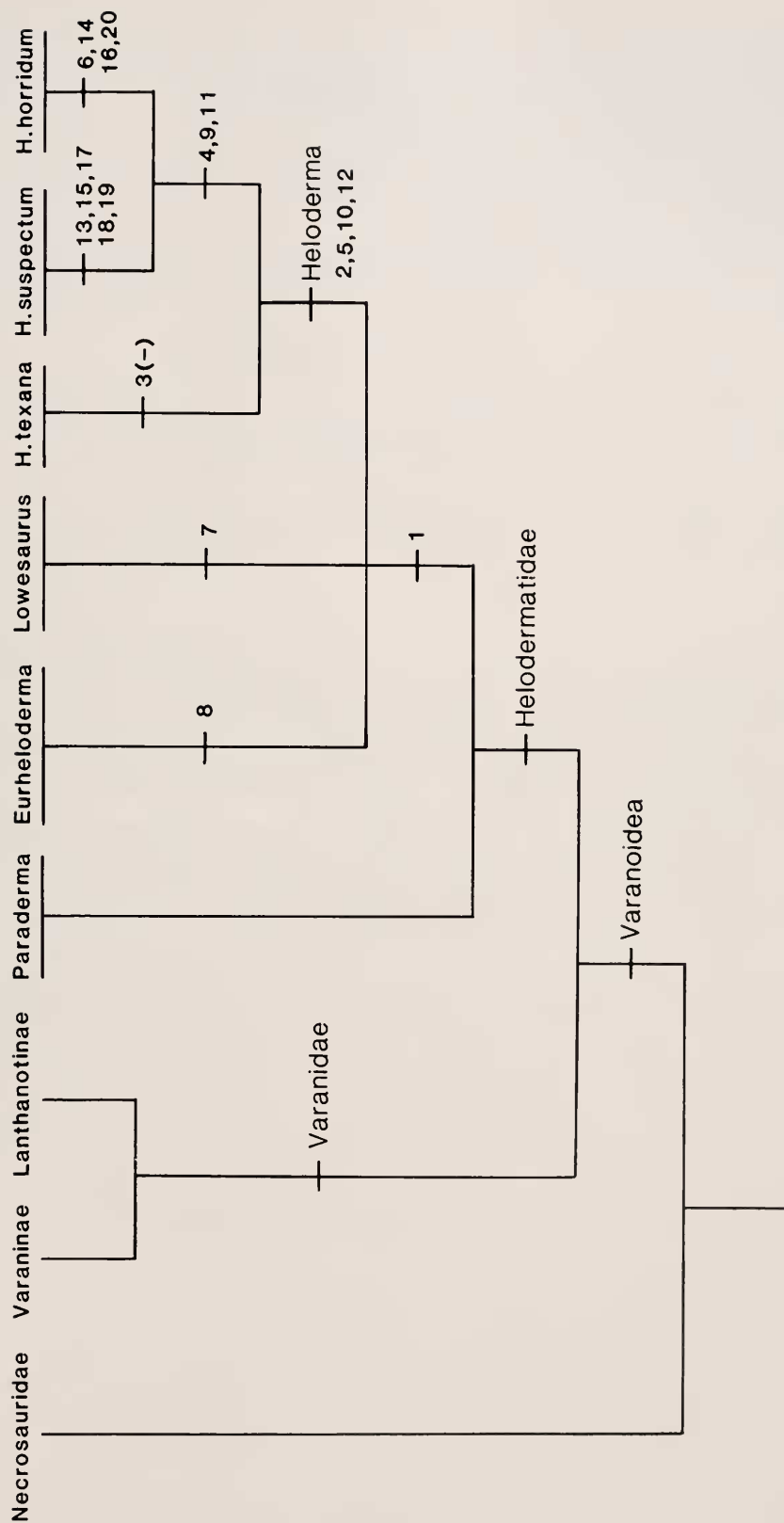


FIGURE 10. The relationships of Helodermatidae as determined from character states in Tables 4 and 5. [PAUP: 43 steps, C.I. = 0.98]

TABLE 4. Character summary of Helodermatidae, scored as ancestral (0), or derived (1). Distribution of character states is presented in Table 5.

1.	Venom groove absent (0), or present and continuous along tooth margin (1).
2.	Base of venom groove narrow (0), or wider than groove itself (1).
3.	Maxillary dental shelf straight (0), or curved medially (1).
4.	Maxillary dental shelf without anterior depression (0), or expanded and depression present (1).
5.	Maxillary teeth greater than nine (0), or equal/less than nine (1).
6.	Maxillary teeth more than seven (0), or seven (1).
7.	Frontal trapezoidal (not triangular) (0), or triangular (1).
8.	Parietal is not strongly constricted medially (0), or is (1).
9.	Vomerine process of palatine extends anterior of last maxillary tooth (0), or not (1).
10.	Osteoderms on skull roof wide, separated by shallow grooves (0), or narrow and smaller, separated by deep grooves (1).
11.	Osteoderms on maxilla larger than those on frontal (0), or equal to them (1).
12.	Cephalic osteoderms mostly flat, vermiculate (0), or domed and tuberculate (1).
13.	Caudal vertebrae 40 or more (0), or less than 40 (1).
14.	Enlarged preanal scales present (0), or absent (1).
15.	Color pattern mottled dark, tail banded (0), or pattern bright pink and black, disrupted (1).
16.	Four phalanges on pedal digit V (0), or three or four phalanges (1).
17.	Body size large, at least 350 mm SVL (0), or small; less than 330 mm SVL (1).
18.	Toes long (0), or short (1).
19.	Habitat preference mesic or semimesic (0), or xeric (1).
20.	Insertion of <i>M. levator pterygoidii</i> extends posterior to columellar fossa (0), or not (1).

hypothesis of phylogenetic relationships. But it also reflects the paucity of fossil material and, hence, our assumptions about the origin of certain characters. For example, without knowledge of the frontal bone of *Eurheloderma* we cannot resolve the position of that taxon relative to *Lowesaurus* and *Heloderma*. Equally, we have assumed that certain features of the frontal that specify Helodermatidae do in fact apply to *Paraderma*, where again that structure is unknown. Naturally, the problem of character origin is most acute with features of soft anatomy.

Yatkola (1976:3) stated that "the overall morphologic similarities between *E. gallicum*, *H. matthewi*, *H. suspectum* and *H. horridum* are more impressive than their differences. Therefore, I have included all four taxa within the genus *Heloderma*." However, we prefer names that indicate monophyly rather than overall similarity. We also wish to avoid redundant names, viz., if all taxa are referred to *Heloderma* then there is no need to recognize another name, Helodermatidae, that specifies the same taxon. We stated above our reasons for recognition of *Lowesaurus*, namely the triangular frontals (character 7). We also retain *Eurheloderma* Hoffstetter for the early Cenozoic species of France because of the distinctively constricted parietal (character 8). *Heloderma* is diagnosed by the wide basal opening of the venom groove (character 2) and morphologically more robust osteoderms (characters 10, 12). *Heloderma texanum* is primitive with respect to *H. horridum* and *H. suspectum* in its absence of: the anterior depression of the maxillary shelf (character 4), the foreshortened vomerine process of the palatine (character 9), and frontal and maxillary osteoderms of equal size (character 11). *Heloderma texanum* is derived compared to other helodermatids in possessing a straight maxillary dental shelf (reversal, character 3).

Derived characters of *Heloderma suspectum* are its bright coloration (character 15), smaller size (character 17), short, non-prehensile tail (character 13), shorter toes (character 18), and occupation of xeric habitats (character 19).

Derived characters of *Heloderma horridum* are its fewer number of maxillary teeth (character 6), insertion of the *M. levator pterygoidii* not extending posterior of the columellar fossa (reversal, character 20), loss of enlarged preanal scales (character 14), variable number of phalanges (three or four) in pedal digit V (character 16).

Although lacking a continuous venom groove (character 1) the late Cretaceous *Paraderma bogerti* is included within Helodermatidae because the jaws are suggestive of a varanoid having a stoutly constructed skull and rounded snout, and it has a dental

TABLE 5. Character distribution within Helodermatidae and outgroups, from Table 4 (1 = derived, 0 = ancestral, 9 = missing data); a phylogeny is shown as Fig. 10.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Varanidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0/1	0/1	0/1	0
Necrosauridae	0	0	0	9	0	0	0	0	0	0	0	0	0	9	9	0	0/1	0	0	9
<i>Paraderma</i>	0	0	1	9	0	0	9	9	9	9	0	0	9	9	9	9	0	0	0	9
<i>Eurheloderma</i>	1	0	1	0	0	0	9	1	9	0	0	0	9	9	9	9	9	0	0	9
<i>Lowsaurus</i>	1	0	1	0	0	0	1	9	9	0	0	0	9	9	9	9	9	0	0	9
<i>H. texanum</i>	1	1	0	0	1	0	0	0	0	1	0	1	9	9	9	9	9	0	0	9
<i>H. suspectum</i>	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	0	1	1	1	0
<i>H. horridum</i>	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	0	0	0	1

morphology that can be interpreted as "early helodermatid." This implies that helodermatids diverged rather early from their varanoid ancestry in a split that primarily favored different predatory modes. In varanines and lanthanotines the skull is considerably narrower than its length, whereas that of helodermatids is nearly as wide as long. McDowell and Bogert (1954) considered the skull of *Heloderma* to be an early stage in a progressive modification of the "platynotan type." As viewed by us, it appears that the morphology of the helodermatid skull probably evolved in response to these squamates using massive, powerful jaws to kill and partially process large, defenseless prey. Varanids on the other hand differentiated as active, searching predators on relatively smaller prey. In this respect, *Paraderma bogerti* appears to be derived in the direction of helodermatids.

By contrast, we can remove *Gobiderma pulchrum* from consideration as a helodermatid. This fossil was described by Borsuk-Bialynicka (1984) from a nearly complete skull and mandible (holotype ZPAL MgR-III/64) and two other partial skulls that were taken from ?middle Campanian Red beds of Khermeen Tsav, Mongolia. *Gobiderma* was featured as a "*Heloderma*-like lizard" although its precise relationship was left unresolved, being designated as a medium-sized "platynotan" of about 5 cm skull length. It differs critically from "necrosaurids" and other varanoids in possessing a flat parietal, one in which the adductors attach to the ventral surface; in this respect it is like *Heloderma*. The osteoderms are small, plate-like and have a pitted surface, but they are fused only to the posterior aspect of the skull. In several other features, however, *Gobiderma* is generalized compared to *Heloderma*: the maxillary segment is tapered, there is no approach or contact of the pre- and postfrontals above the orbit, and it retains the upper temporal arch. Actually, the overall appearance of the skull recalls that of *Xenosaurus*. In appreciating the peculiarities of this taxon, Borsuk-Bialynicka (1984) offered that it might have been "an Asiatic substitute of the American group [rather] than a group ancestral to the Helodermatidae." The external nares are not at all retracted in the manner of varanoids, nor do the subolfactory processes of the frontal exhibit the characteristic downgrowth and ventromedial contact. The tooth row is nearly entirely antorbital, although the maxilla appears to participate in the suborbital fenestra, to judge from her figures, plates and descriptions (Borsuk-Bialynicka 1984). We also leave this taxon unassigned pending further study of "Platynota" and Necrosauridae.

III. AN EVOLUTIONARY SCENARIO FOR HELODERMATIDAE

The goal of this section is to offer a natural history perspective of helodermatids that is consistent with their fossil history, phylogeny, ecology, and behavior. We make no attempt to invoke a particular process (e.g., natural selection) for the origin of adaptive patterns (*cf.* Greene 1986). Our remarks are based on the phylogenetic analysis presented above, information in the literature, examination of stomach contents, casual observations on captive individuals, and unpublished observations provided by others. We are interested in identifying concordant changes in natural history and morphology through evolutionary time. Therefore, the discussion proceeds from higher taxa to the

species of helodermatids themselves. Because the relationships of varanoids to other anguimorphs are controversial, we rely on general attributes of anguids and xenosaurids to postulate the polarities of ecological and behavioral characteristics.

Natural History of Anguids and Xenosaurids

Relative to other living squamates (Pough 1980), anguids range in size from rather small (e.g., SVL of 55–70 mm in *Elgaria parva* Knight and Scudday 1985) to moderately large (more than 500 mm total length in *Ophisaurus apodus* and some *Diploglossus*). A few species are fossorial (e.g., *Anniella*), but most are terrestrial (*E. coerulea*) or arboreal (*Abronia*). A semiprehensile tail is probably primitive for anguids (Greene 1986). Most anguids are probably insectivorous, but some are known occasionally to eat vertebrates, for example *E. multicaudata* (Cunningham 1956). The anguid tongue is modified for chemoreception (Schwenk 1984) and likely plays a prominent role in finding and/or recognizing food. Greene (in Burghardt 1978) demonstrated innate chemically mediated recognition of prey by naive *Gerrhonotus liocephalus*. For reviews of lizard feeding biology see Greene (1982), Pough (1973), Regal (1978), and Stamps (1977).

The New World xenosaurids inhabit crevices in rocks and trees (Alvarez del Toro 1982, King and Thompson 1968). In captivity they are secretive and active nocturnally (*personal observation*). Presch (1981) reported an iguanid lizard (*Sceloporus*) in the stomach of a *Xenosaurus grandis* from Mexico, although several dozen other stomachs of this species from the same locality yielded only a variety of insects (Greene and McDiarmid, unpubl. data). The only Old World xenosaurid, *Shinisaurus crocodilurus*, lives along streams where it feeds on tadpoles, fish and aquatic invertebrates. It bites powerfully if restrained (J. B. Murphy, *personal communication*).

A number of antipredator responses are so widespread among anguids and xenosaurids (as well as varanoids; *see below*) that they are surely ancestral for Anguimorpha. These squamates characteristically are cryptic, being of drab dorsal color that is marked by some type of disruptive pattern (e.g., cross bars). When threatened they attempt to flee towards the nearest retreat; if seized, they struggle violently, defecate copiously, hiss, gape and bite fiercely. The tail is autotomic in anguids (aside from *Ophisaurus apodus*) and *Shinisaurus*, but not in *Xenosaurus* (*see* Greene, MSa, for a review of defense behavior in lizards).

Natural History of Varanus and Lanthanotus

Varanids are small to very large lizards (*Varanus brevicauda*, total length 24 cm vs. *V. komodoensis*, total length 3 m). The extinct *Megalania prisca* from the Quaternary of Australia is thought to have achieved a total length of 6 m (Hecht 1975). Judging from stomach contents of living species, an ancestral varanid was moderately large, terrestrial or semiarboreal, and fed on a variety of small invertebrates and vertebrates. Gigantism and consumption of relatively large vertebrates (mammals in the case of varanids) are probably derived attributes within Varanidae, as is extremely small size (Losos and Greene MS). Varanids have tongues that are highly modified for chemoreception (Schwenk 1984) and apparently are used to locate hidden prey during their wide search activities (Auffenberg 1981, Pianka 1982, Losos and Greene MS). Varanids are cryptic, wary, and fast moving lizards that exhibit stereotyped threat postures when cornered. If approached or handled they lash with the tail, gape, hiss, struggle, defecate, and bite (Greene MSa).

Almost nothing is known about the natural history of *Lanthanotus borneensis*. Apparently it is a specialized burrower, but swims well and has a partially prehensile tail (Proud 1978, Sprackland 1972). A specimen in the Museum of Comparative Zoology had earthworm setae in its gut (Greene, *unpublished data*). Captives flatten their body when threatened, and when handled struggle, defecate, hiss, and sometimes bite (Greene MSa).

Natural History of Living Helodermatids

Behaviorally and morphologically helodermatids are in some respects generalized varanoids. Like other anguimorphs and unlike varanids, the two living helodermatids prefer relatively cool temperatures (John-Alder et al. 1983). They are not as agile as varanids, yet not so clumsy as often portrayed. The popular vision of a rotund, sluggish beast stems from the appearance of captive specimens (usually *Heloderma suspectum*) that have been housed in small cages and fed a diet of infertile chicken eggs. It is true that Gila monsters (*H. suspectum*), being shorter and stouter, resemble this portrait more so than do Beaded lizards (*H. horridum*). Our observations on both species are consistent with those of John-Alder et al. (1983), that these animals cannot capture an adult, uninjured rodent except in a very confined space. Nevertheless, helodermatids typically take a broader range of prey than is implied by the usual captive diet. Freshly collected individuals, especially *H. horridum*, are rarely, if ever, obese.

Bogert and Martín del Campo (1956) summarized records for natural prey of *Heloderma horridum*, based on stomach and/or intestinal contents of 20 animals. These consisted of five mammals, including a rabbit (*Sylvilagus* sp.) and a cotton rat (*Sigmodon* sp.) found in one stomach; two birds including a nestling squirrel cuckoo (*Piaya cayana*); ten sets of bird eggs, numbering up to 13 per stomach and possibly including those of unidentified doves and Douglas quail (*Lophortyx douglasi*); two sets of reptile eggs, numbering up to 35 per stomach, including those of an unidentified lizard and of a turtle (*Kinosternon*); and six sets of insect parts that the authors discounted as likely to have been ingested accidentally. Bogert and Martín del Campo (1956) also noted that some *H. horridum* they examined were juveniles, suggesting, perhaps, that there are no major ontogenetic changes in diet. In the KU and Los Angeles County Museum collections we examined the stomachs of five beaded lizards that contained prey, the food items consisting of two sets of reptile eggs, a set of bird eggs, and two sets of large coleopteran larvae (includes items mentioned by McDiarmid 1963).

Bogert and Martín del Campo (1956) also summarized published observations on the natural prey of 11 *Heloderma suspectum*. They found 14 mammals (ground squirrels and rabbits) in nine animals, reptile eggs in four, bird eggs in one, and a lizard in one. Using radiotelemetry, Jones (1983) studied the foraging biology of nine *H. suspectum* in Arizona. The individuals he followed hunted over wide areas, and consumed 24 sets of quail eggs, two sets of dove eggs, and three mammals, or groups of mammals.

The climbing habits of helodermatids have been known for some time (Bogert and Martín del Campo 1956), but only recently has there been substantial evidence to document this activity. Cross and Rand (1979) observed two *Heloderma suspectum* for more than 15 hours, and witnessed each animal ascend and descend the rough bark of a desert willow; in one case the tail was used in locomotion. Alvarez del Toro (1982) described climbing behavior and semiprehensile use of the tail by captive *H. horridum* collected from Chiapas, Mexico. J. W. Hardy (*personal communication*) found adult *H. horridum* raiding the nests of Beechey's jay (*Cissilophya beecheyi*), high in trees in Nayarit, Mexico.

Greene raised a juvenile *Heloderma horridum* (initial weight ca. 55 grams) from Colima, and observed frequent arboreal activity. The lizard was kept in a 20 gal aquarium containing a hollow limb that extended from one bottom corner diagonally up to the opposite corner. The beaded lizard spent most of its time concealed in a cavity at the upper extent of the limb, emerging only to feed and drink. It climbed without difficulty, and curled its tail about branches when descending. Ambulatory juvenile mice were chased and subdued without obvious difficulty, albeit somewhat clumsily.

Helodermatids spend large amounts of time in underground burrows (Bogert and Martín del Campo 1956, Cross and Rand 1979, Jones 1983); they are potentially more vulnerable to predators when hunting. If threatened, individuals of both species usually flee towards shelter in a bush or burrow. An adult *Heloderma horridum* in Oaxaca, México, rapidly ascended a pine tree when it was approached (V. Fitch, *personal*

communication). If a helodermatid is aggravated or handled, it hisses, gapes, struggles, and bites (Bogert and Martín del Campo 1956).

Adaptive Trends among Varanoidea

Anguimorphs probably began as terrestrial and semiarboreal squamates in tropical or subtropical mid-latitudes of Laurasia during the late Mesozoic (*see above and Estes 1983b*). They fed predominantly on insects that were encountered by searching actively, using both visual and chemical cues. Larger species preyed on large insects and the occasional small vertebrate. Primitively, varanoids were larger than other anguimorphs, and more widely foraging. Likely, they relied more on chemoreception for locating prey and took vertebrates more often, but these were probably small relative to their body size. The defensive behavior of helodermatids and *Lanthanotus* is similar to that of anguids and xenosaurids, and except for venom use in helodermatids, is likely to represent an ancestral anguimorph response.

The adaptive zone of monitor lizards (*Varanus*) is specialized beyond the primitive varanoid condition. Physiologically these animals are capable of unusual locomotor stamina (Bennett (1978), they prefer high temperatures, and travel extensively while hunting (Auffenberg 1981, Losos and Greene MS, Pianka 1982). Predation on large mammalian prey (e.g., by *Varanus komodoensis*, Auffenberg 1981) is a derived condition within Varanidae, and involves ingestion of pieces rather than large, intact items. The living members of the subfamily exhibit considerable ecological diversity (Auffenberg 1981, Greene 1986) although most species are reasonably similar in their feeding biology (Losos and Greene MS).

What little is known about *Lanthanotus borneensis* suggests that this bizarre creature is a burrower. For instance certain cranial features shared with other anguimorphs are associated with fossoriality (Borsuk-Bialynicka 1984, Gauthier 1982, Rieppel 1983). If some or all of the synapomorphies of Lanthanotinae are functionally related to fossoriality, they represent an adaptive shift that is unique in the evolution of varanoids.

Available information shows that living helodermatids take a potential range of prey types, from vertebrate eggs to large insect larvae, and that mammals are of major importance. Although complete comparative data are lacking, it appears that both species may take relatively larger, intact prey than any other living squamate aside from some snakes (Stahnke 1952, Greene 1982, 1983). Hunting is characterized by wide searches and investigating specific sites in terrestrial and arboreal microhabitats (*see above and Bogert and Martín del Campo 1956, Jones 1983*).

There is evidence that tissue-destructive venoms of viperid snakes facilitate digestion of large, bulky prey, especially under conditions like mild temperature where such items might putrify prior to digestion by intestinal secretions (Greene 1983, MSb, Pough and Groves 1983, Thomas and Pough 1979). Venom injection is a derived characteristic of Helodermatidae, developed most fully in *Heloderma*, and we suggest that it is an adaptation for preying on large, bulky vertebrates under temperature regimes that are periodically cool. Information on the venom of helodermatids is incomplete, sometimes contradictory (Russell and Bogert 1981), and controlled studies using natural prey would be of great interest.

Evolutionary trends in diet parallel morphologies of the tongue and throat region of Varanoidea (McDowell 1972, Schwenk 1984). Anguimorphs primitively have a tongue that is functionally and structurally divided, such that the hind-tongue functions in food transport and the foretongue serves as a chemoreceptor (via taste buds, Schwenk 1984) and a vehicle for carrying odor molecules to the vomeronasal organ. McDowell (1972) noted that helodermatids show features plausibly related to increased gape (e.g., reduction of the posterior limbs of the tongue), and suggested that the tongue of *Lanthanotus* is used to swallow "less bulky food" than that of helodermatids. The tongue of *Varanus* is highly derived and protrusible; it serves a chemoreceptive role and no longer functions in frictional food transport. Swallowing in monitors results entirely

from throat compression, lateral movements of the neck, and esophageal peristalsis (Smith 1986).

Bogert and Martín del Campo (1956) commented that in helodermatids venom was certainly not necessary to immobilize prey and, because it is clearly associated with the bite, they hypothesized that venom and teeth are primarily a means for thwarting predation. That explanation is consistent with other research demonstrating that wide foraging habits and preoccupied feeding techniques (e.g., digging for prey) often correspond with increased risk of predation (Huey and Pianka 1981, Vitt 1983), and the evolution of defensive specializations (Greene MSA). We favor the hypothesis that venom delivery in helodermatids evolved in a feeding context and was later co-opted for defense under some circumstances (*see below*). However, a decisive choice between these alternatives is as yet not possible.

The two living species of *Heloderma* differ mainly in three characteristics. *Heloderma horridum* has a higher mean number of subdigital scales and a longer tail. An increased number of subdigital lamellae is associated with arboreality in certain other lizards (*Anolis*, Collette 1961; *Aristelliger*, Hecht 1952). However, high lamellar counts and arboreality are also correlated with increased body size in those taxa and in *H. horridum*, thus obscuring functional interpretations and character state polarities. To judge from other anguimorphs, including varanids (Mertens 1942, Greene 1986), the high subdigital scale counts and the comparatively long, semiprehensile tail of *H. horridum* are primitive for varanids, and probably anguimorphs. They need not be explained as specializations arising in *Heloderma*. The short tail and toes of *H. suspectum* are derived attributes, perhaps associated with fat storage and digging for prey, respectively.

Heloderma horridum is a predominantly black animal with irregular yellow markings on the body and yellow rings on the tail [adult *H. h. alvarezi* are entirely black, whereas juveniles are patterned like adults of other subspecies (Alvarez del Toro 1982)]; *H. suspectum* is a black and pink animal, the latter color often predominating. A mottled, cryptic dorsal pattern and a ringed tail, as in *H. horridum*, are probably ancestral for anguimorphs (Gauthier 1982, Greene 1986). The more brightly contrasting pattern of *H. suspectum* is clearly derived; it is probably both cryptic and aposematic (Bogert and Martín del Campo 1956), and functionally coupled with the venomous bite.

The moderate diversity and fairly widespread occurrence of helodermatids in North America and Europe during the late Cretaceous and early and middle Tertiary suggest that they inhabited a once broader spectrum of environments than would be inferred from their present distribution. Our analysis indicates that primitively these venomous varanoids inhabited non-desert environments, and that among the two living species the habits and habitat of *Heloderma horridum* are more representative of an ancestral helodermatid. The few derived attributes of *H. suspectum* are associated with the xeric, open conditions characteristic of the latest Cenozoic in southwestern North America.

Although they resemble ancestral varanoids in several respects, helodermatids exhibit morphological and natural history traits that are derived and unique among all other living squamates. Our appraisal of their known history and biology suggests that the extant species are appropriately regarded as living fossils.

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